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VERTEBRATE FOOTPRINTS AND INVERTEBRATE TRACES FROM THE CHADRONIAN (LATE EOCENE) OF TRANS-PECOS TEXAS

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CONTENTS

*Note: The symbol ◊ identifies ichnogenera and ichnospecies not represented in the West Texas assemblages.

ABSTRACT

An assemblage of footprints from a late Eocene (Chadronian) tuff in Presidio County, west Texas, constitutes the richest terrestrial ichnofauna yet to be reported from the North American Tertiary. It consists largely of the tracks of vertebrates, including turtles, large and small birds, and a variety of large and small mammals. In addition, two types of invertebrate traces are present. The turtle tracks are attributed to two new ichnospecies, *Chelonipus chadronicus* and *C. parvus*, and are placed in the new morphofamily Chelonipedidae. Proposals are advanced for the overhaul of the present classification of avian tracks. The new morphofamilies Gruipedidae, Charadriipedidae, Avipedidae, and Anatipedidae are proposed. Emended diagnoses are formulated for the ichnogenera *Gruipeda* Panin and Avram, ◊*Ardeipeda* Panin and Avram, ◊*Charadriipeda* Panin and Avram, *Avipeda* Vialov, and ◊*Anatipeda* Panin and Avram, and their type species. The new genus *Fuscinapeda* is proposed and its type species, ◊*F. sirin* (Vialov), emended. Three new species, *Gruipeda calcarifera*, ◊*Fuscinapeda meunierii* and *F. texana*, are proposed, and two other avian footprint morphotypes are also described.

Nineteen morphotypes of mammalian footprints are distinguished. The majority are placed in new ichnogenera and species. These include *Schyromorphipus oxypages*, probably an insectivore; *Zanclonychopus cinicalcator*, a creodont; five carnivores, one (*Tetrastoibopus phoros*) surely and another (*Falcatipes floriformis*) probably miacids, one probably a mustelid (*Phacelopus therates*), and two probably amphicyonids (*Axiciapes ferox* and *A. curvidigitatus*); a likely mesonychian (*Corymbipes superstes*); three types of perissodactyls, including a tapiroid (*Apoxypus tessellatus*) and a rhinocerotoid (*Thrinaxopus hoplephoreus*); a problematic footprint, possibly also a perissodactyl or a creodont (*Palimmecopus praecursor*); two artiodactyls, a probable entelodont (*Anoplotheriipus zeuctus*) and camel-like tracks (*Gambapes hastatus*); four types of rodent tracks, of which two (*Tricorynopus elaphrus* and *Ptyariopus aichmanticheirus*, the latter considered to be an ischyromyid) are named. One footprint morphotype remains of uncertain systematic affinity.

We emend the ichnogenus ◊*Bestiopeda* Vialov and propose a new ichnogenus, ◊*Chelipus*, to accommodate one of Vialov's species no longer attributable to ◊*Bestiopeda*. We offer emended diagnoses for the artiodactyl ichnogenera ◊*Pecoripeda* Vialov, ◊*Odocoileinichnium* Aramayo and Bianco, and ◊*Lamaichnium* Aramayo and Bianco. We elevate ◊*Cervipeda* Vialov from subgeneric to generic status and emend it.

Two morphotypes of invertebrate traces are reported. One appears to represent the footprint trail of a terrestrial arthropod; the other is of uncertain character.

INTRODUCTION

This paper describes a unique assemblage of footprints exposed in a remote area of Presidio County, Texas. The tracks were implanted in freshly fallen volcanic ash that had been recently wetted by rains to form a mud flat. The ash layers subsequently solidified to form a very hard, light green tuff, 3 m (10 ft) thick. This bed crops out near the western limit of the Bracks Rhyolite of the Vieja Group (Wilson, 1986). Because that volcanic unit lies stratigraphically between the Chambers Tuff below and the Capote Mountain Tuff above, the footprint-bearing layers may be situated either in the uppermost part of the Chambers Tuff or at the bottom of the Capote Mountain Tuff. The Bracks Rhyolite has been dated between 36.3 and 38.7 million years old (Henry et al., 1986); thus the footprint-bearing tuff is attributed to the Chadronian Land Mammal age (NALM), long regarded as early Oligocene but recently assigned to the late Eocene (Prothero and Swisher, 1989).

Wilson and associates have described the extensive vertebrate faunas from the Trans-Pecos area of west Texas in a series of reports (for a review of previous work and references, see Wilson, 1978, 1986). Four Chadronian local faunas have been identified. In ascending order, they are Porvenir, Little Egypt, Airstrip and Ash Spring. The Porvenir and Little Egypt local fauna and the approximately equivalent Rancho Gaitan local fauna from northeastern Chihuahua, Mexico (Ferrusquia-V. and Wood, 1969), are closest stratigraphically to the Bracks Rhyolite and may thus bear the closest relationship with the animals that made the tracks described herein.

The track-bearing tuff occurs as a series of gently dipping strata that are well exposed in the bottoms of intermittently flowing streams (see pl. 1a). The massive rock does not split into slabs, so tracks cannot easily be removed. Instead, casts of selected examples were made, together with the intervening rock surfaces, and these replicas furnish the basis for this report.

The field work for this study was conducted in 1975 under the supervision (and with the active participation) of Professor John A. Wilson

of The University of Texas at Austin, with financial support from the National Geographic Society (Wilson, 1984). Casting of the tracks was carried out in late March, because later in the season the rocks in west Texas become too hot to permit the use of molding compound.

METHODS

The tracks were mapped in the field by plane table and alidade (data on file in the Vertebrate Paleontology Laboratory of the Texas Memorial Museum, The University of Texas at Austin and at the Department of Geological Sciences at The University of Saskatchewan, Saskatoon).

Flexible molds of Smooth-On #100 Flexible Mold Compound 2343 were made of tracks at eleven of fourteen known localities (see pl. 1b, 2a). Soon afterward, before the molds could become distorted, high quality plaster or fiberglass casts were made from them. At one locality, the footprint-covered surface was so large (about 2.7 m x 5.5 m) that the molds were made in six sections (see pl. 2b, 3). These sections were reunited in the laboratory to create what we have termed the "Grand Junction" slab. Smaller sets of tracks were cast as single units.

Both molds and casts are housed in the Vertebrate Paleontology Laboratory in Austin. The slabs have been assigned the numbers TMM 41500-13 to 27. Such numbers ordinarily identify specific slabs; however, in the "Grand Junction" slab with its many crisscrossing tracks, letters A to F have been assigned to the six sections, followed by a number which designates the placement of the footprint, or footprints, on the slab. The "Grand Junction" slab is illustrated in pl. 4 and a key to the numbering system is given in fig. 52, placed at the end of this account for ready reference.

Before the scientific discovery of the footprints, some unknown collector had found and attempted to remove some of the tracks by hammer and chisel. In the process, several tracks had been ruined. Since the track site is too remote to be effectively protected, the footprints are in danger of being wholly destroyed in the future by vandals. Because of this, we do not give precise locality information here. The site is identified only by its site number, 41500. However, locality data are on file at the Vertebrate Paleontology Laboratory in Austin and will be furnished to qualified persons.

Taxonomic considerations have impelled us to take account of ichnogenera and ichnospecies not represented in the west Texas assemblages. To avoid confusion, such non-Texan taxa are distinguished by the symbol ◊.

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SYSTEMATIC PALEONTOLOGY

I. VERTEBRATE FOOTPRINTS

The description, and in particular the classification, of fossil vertebrate footprints presents considerable difficulties (see discussion in Sarjeant, 1975:295-300; Sarjeant, 1989, 1990; Scrivner and Bottjer, 1986). There are two different approaches. One is to try, by identifying the trackmakers, to classify footprint ichnotaxa into the Linnaean system of families, orders, and classes (based on osteological morphology), as attempted in part by Kuhn (1958). The other is to adopt the hierarchy of names specifically designated for trace fossils by Vialov (1966, 1972) whose system mirrors, but does not correspond with, the standard zoological classification. The latter approach has been employed recently, with modifications, by Scrivner and Bottjer (1986). An intermediate procedure was utilized by Haubold (1971), who placed ichnologically based families into osteologically based higher taxa where such families had been proposed, but otherwise assembled the ichnogenera into osteologically based families.

A problem for vertebrate paleoichnologists examining Tertiary assemblages is inadequate knowledge of the osteology of the feet, which is often known only in broadest terms or not at all. This is particularly true of the vertebrate faunas, described by Wilson and others, from the Chambers and Capote Mountain Tuffs dealt with in this paper. (For faunal lists see Wilson, 1986, and references therein). However, by the use of geologically later analogues and careful interpretation of footprint patterns, most of the tracks described here can be shown to accord with certain genera and species of mammals identified by Wilson (1978) from contemporaneous strata in the same general area.

The organization of reptilian footprints into morphofamilies, although foreshadowed earlier, began effectively with the work of Lull (1904), who assembled Triassic tracks from the Connecticut Valley into families with names based upon ichnogenera, not upon osteological genera. However, his approach has been only inconsistently adopted by subsequent workers, many footprint ichnogenera being at present merely placed loosely into osteologically based superfamilies or higher taxa. For reasons set forth in earlier papers (Sarjeant and Kennedy, 1973; Sarjeant, 1975), Lull's approach is here preferred.

For the mammal footprints, the compromise approach of Haubold (1971) is adopted, since this gives the best impression of the zoological constitution of the community of animals that made the tracks. For the bird prints, in contrast, no similar confidence in identification of the trackmakers is possible; a purely morphological classification is therefore proposed that only crudely approximates the natural relationships among Aves.

In vertebrate paleontology the convention is that, when a monogeneric family or a monospecific genus is described, no separate diagnosis is presented for the subordinate taxon. That approach is reasonable in a classification that represents clearly ascertainable affinities and precisely determinable morphological characteristics, genetically controlled. In paleoichnology, in contrast, we are dealing with what are, after all, mere structures in sediment, however generated (Sarjeant, 1990). Comparable morphologies of pedal undersurfaces may occur in groups that are not especially close phylogenetically. Moreover, the characteristics will be altered by behavior. Consequently, the identity of the trackmaker is only rarely capable of precise determination. Ichnofamilies, ichnogenera and even ichnospecies have an essentially arbitrary delimitation, the limits of the higher categories embracing the lower, but not necessarily incorporating all characteristics of those lower categories. Moreover, our knowledge of Tertiary terrestrial paleoichnology remains meager.

Since the definition of ichnotaxa is so much more arbitrary than that of Linnaean taxa, paleoichnologists have come to adopt an approach different from that of vertebrate paleontologists. Diagnoses of ichnofamilies are broad, specifying only the features considered essential for their recognition; diagnoses of ichnogenera are narrower, but again they incorporate merely the features that are considered significant. Only in the definition of ichnospecies are all relevant characteristics specified. In conformity with this philosophy, separate diagnoses are here presented for each hierarchical rank, even within monogeneric families and monospecific genera, to clarify our opinions on what features are important for the recognition of each taxon and to allow for an expansion of content of the higher categories when further Cenozoic ichnofaunas are described.

The descriptive approaches we have adopted correspond to those advocated by Leonardi et al. (1987) and Sarjeant (1988). In particular, measurements of whole footprints and of trackways agree with Plate I of Leonardi et al.; those of parts of the footprint accord with their Plate V; and measurements of interdigital angles are taken as indicated in their Plate VI. For definitions of terms, Leonardi et al. (1987:43-51) should be consulted.

However, no standard has been set for characterizing the relative length of the stride or the relative breadth of the trackway, the two parameters that differentiate efficient from inefficient pedestrians. Consequently we propose the following, the pes being preferred to the manus as standard for measurement because, where they differ in size, the pes is usually larger:

Breadth of Trackway:
- Broad: greater than three times width of pes
- Moderate: one to three pes widths
- Narrow: less than one pes width

Stride:
- Long: 5 times length of pes or greater
- Moderate: 3 to 4.9 times length of pes
- Short: less than 3 times length of pes

We prefer to employ such an approximate terminology for trackway proportions since even subtle changes in speed of movement can render greater precision meaningless. In an efficient pedestrian, for example, the stride length would be long at a walking pace, but still longer at a run; the breadth of trackway, though always narrow, would become narrower. The trackway breadth of an inefficient pedestrian would remain broad if its speed slowed, but its stride would shorten further (fig. 1 exemplifies this well). Yet our characterization of these parameters still serves to differentiate their relative efficiency as pedestrians.

It should be stressed that, in measuring these parameters in any trackway where stride lengths change, the longer stride should be measured rather than the shorter, since a shortening of stride merely indicates a slackening of pace and may precede a complete halt. (For an example of such changing pace, see pl. 8b, the avian trackmaker having halted and then walked forward).

CLASS REPTILIA
ORDER TESTUDINES

Morphofamily Chelonipedidae
Sarjeant and Langston, nov.

Diagnosis. Quadrupedal footprints with trackway very broad and stride short. Semiplantigrade to digitigrade; footprints broader than long and digits stiff and very short, bearing short, often blunt claws.

Type Genus. *Chelonipus* Rühle von Lilienstern, 1939. Triassic, Germany.

Remarks. Many Paleozoic amphibians have a broad trackway and short stride, but their footprints differ from those of chelonians by exhibiting longer, more flexible digits without claws. In most instances, moreover, such footprints are plantigrade rather than semiplantigrade to digitigrade.

We do not consider the lack of plastron impressions important, because their presence or absence would be a consequence of behavior. Indeed, such impressions have not yet been reported from the fossil record.

Ichnogenus *Chelonipus*
Rühle von Lilienstern, 1939.

Chelonipus chadronicus
Sarjeant and Langston, ichnosp. nov.

Plate 5. Figures 1, 2.

Derivation of Name. After the Chadronian NALM age of the late Eocene.

Diagnosis. Quadrupedal footprints exhibiting a broad trackway and short stride. Foot-

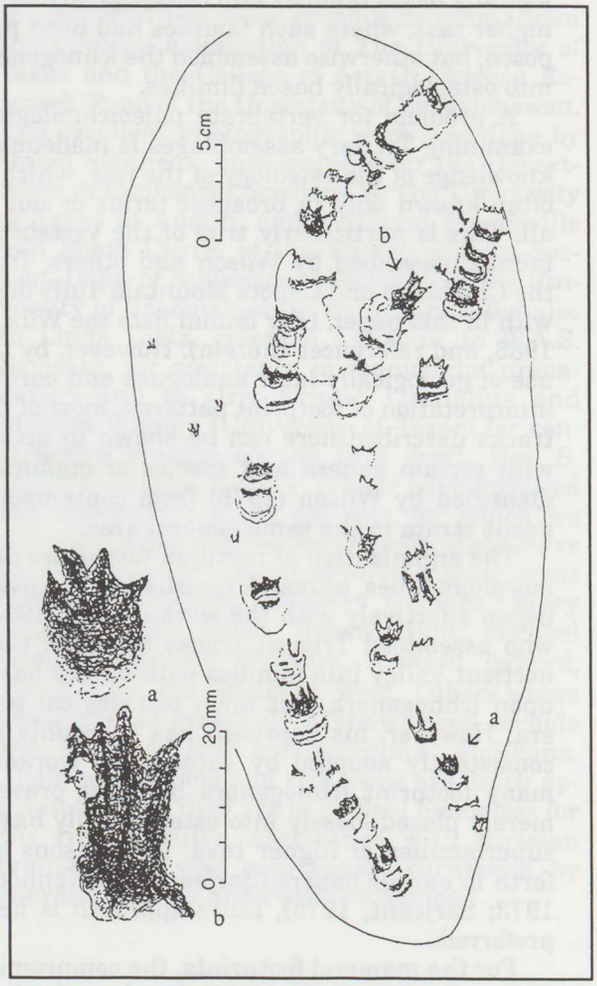


Figure 1. *Chelonipus chadronicus* Sarjeant and Langston, ichnosp. nov., TMM 41500-40. (a) Right manus. (b) Right pes, superposed on an earlier manus print.

prints vary with the animal's behavior from digitigrade to semiplantigrade. In both manus and pes, four digits are normally impressed, the fifth (V) rarely being impressed. All digits are clawed. Pollex short; digit II almost twice as long as pollex and curved inwardly; digits III and IV of intermediate length, digit III directed forward and digit IV outward. Digits I to III of pes directed forward, the hallux and digit II shorter than digit III; digit IV outwardly directed and with a longer claw. Webbing present between all these digits. Tail-drag impressions lacking.

Type Specimen. TMM 41500-40 on slab 41500-18.

Horizon and Locality. See Introduction.

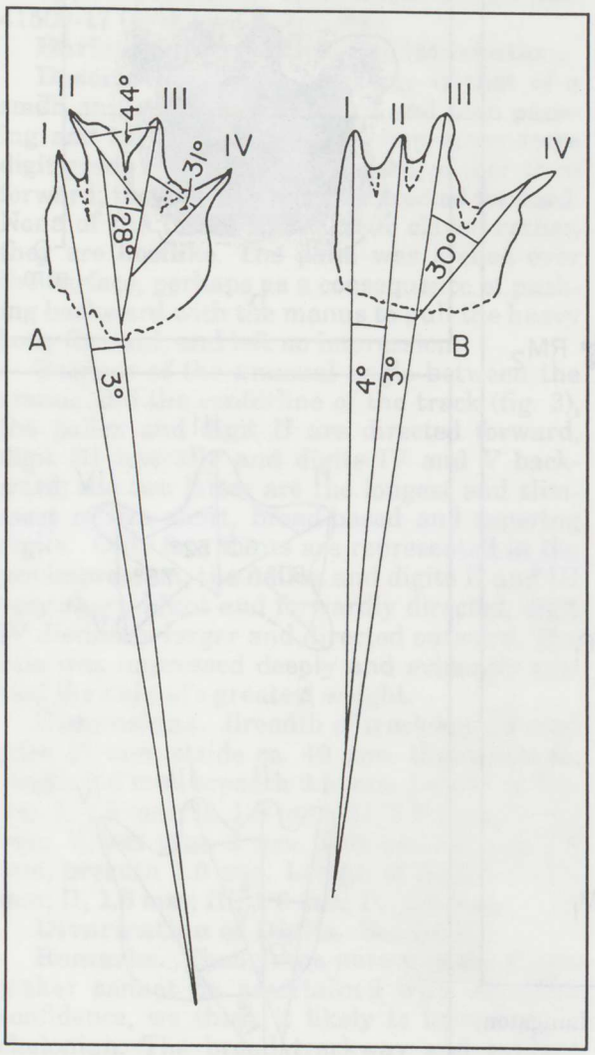


Figure 2. *Chelonipus chadronicus* Sarjeant and Langston, ichnosp. nov., TMM 41500-40. Interdigital angles. (a) Right manus. (b) Right pes.

Description. The trackway is that of a turtle walking at first steadily, then slowing (or stopping) and turning. The variable behavior produced impressions varying from semiplantigrade to digitigrade with prints often superposed. Digitigrade impressions exhibit only three claws—of digits II to III of the manus and I, III and IV of the pes. In contrast, the better semidigitigrade to semiplantigrade imprints represent four digits (I to IV). In one instance (pl. 5d; fig. 2b) a backward prolongation of the manus may represent a backwardly-turned fifth digit (V), but it is more likely to be simply a drag-mark.

The pollex is short and tapering, directed almost forward. Digit II of the manus is larger and stronger than the others, tapering only at its inwardly directed distal end. Digit III is shorter and forwardly directed, digit IV somewhat slimmer. All four manual digits bear sharply pointed claws of similar length.

The first three digits of the pes have blunter claws, that of digit III especially so; digit IV, in contrast, has a long, sharp claw directed outward. The hallux and digit II are relatively short, digit III decidedly longer; digit IV is the thickest of the hind-foot digits.

Dimensions. Breadth of trackway 72 mm; pace 76 mm; stride (based on hind-feet) 40 mm. Manus: length 18 mm; breadth 14 mm. Length of digits: I, 3mm; II, 6 mm; III, 4.5 mm; IV, 3.5 mm. Pes: length ca. 13.8 mm, breadth 16.25 mm. Length of digits: I, 3 mm; II, 3.5 mm; III, 4.25 mm; IV, 6 mm.

Divarication of Digits. See fig. 2.

Remarks. Tracks of turtles, though common enough today, have been described only rarely from the fossil record. Two of the described species of this ichnogenus (*Chelonipus torquatus* Rühle von Lilienstern, 1939, and *C. pleiningeri* Haubold, 1970) were reported from the Triassic; the former shows very blunt claws, the latter much sharper claws with a stronger curvature. A third ichnospecies, *Emydichnium megapodium* (Walther, 1904; Nopcsa, 1923) from the German Jurassic, embraces chelonoid footprints of much larger size than those here discussed, but is not well enough described or figured for detailed comparison.

The rather sprawling and uncertain gait of *Chelonipus chadronicus* suggests an amphibious turtle rather than an habitually terrestrial one. Since Van Brackle (1978) has identified the remains of turtles from the adjacent Chambers Tuff as either the semi-aquatic *Stylemys* or the terrestrial *Geochelone* or *Gopherus*, *Stylemys* is favored here as the trackmaker.

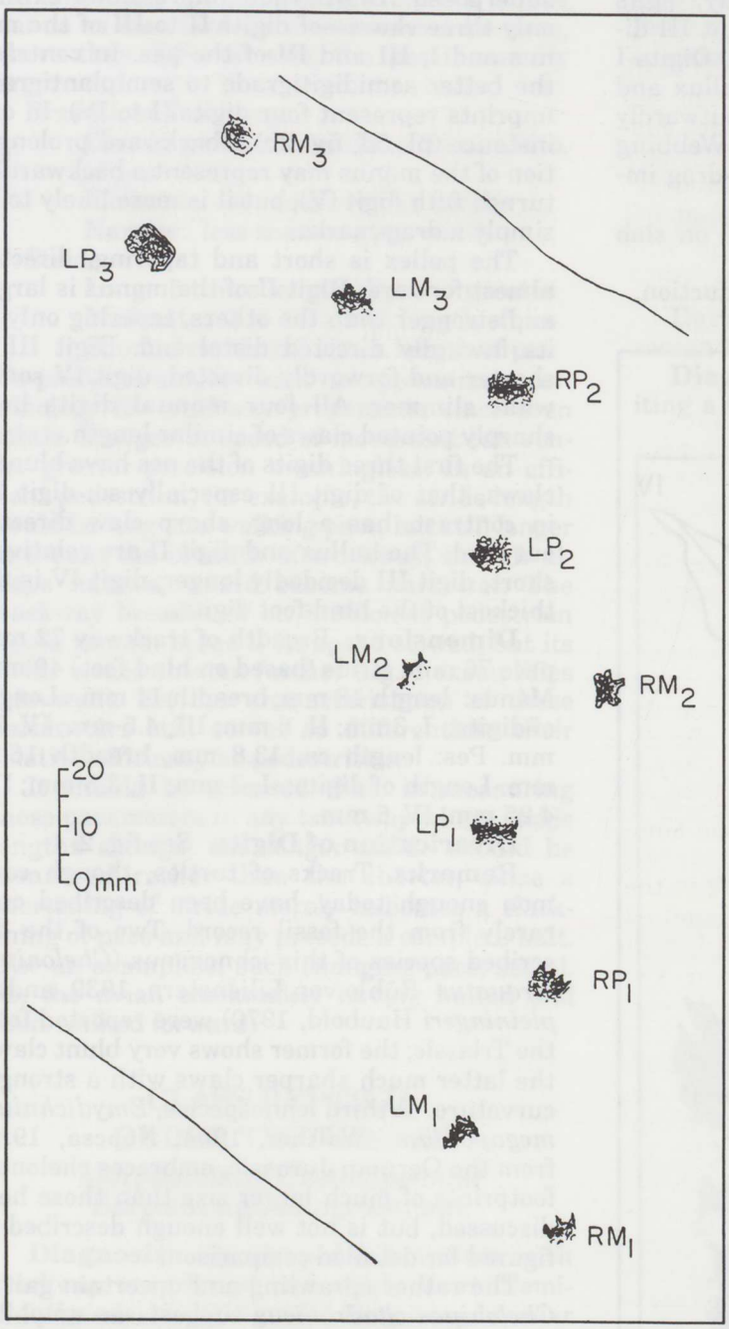


Figure 3. (Above) *Chelonipus parvus* Sarjeant and Langston, ichnosp. nov., TMM 41500-23. Entire trackway.

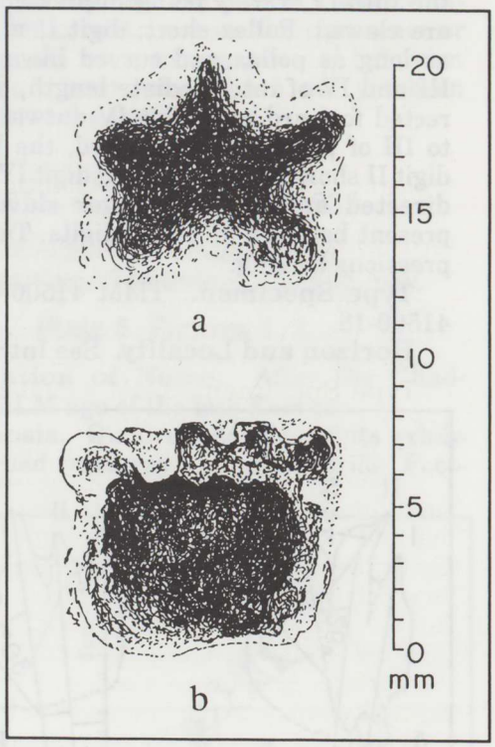


Figure 4. (Top right) *Chelonipus parvus* Sarjeant and Langston, TMM 41500-23. (a) Detail of right manus. (b) Detail of left pes.

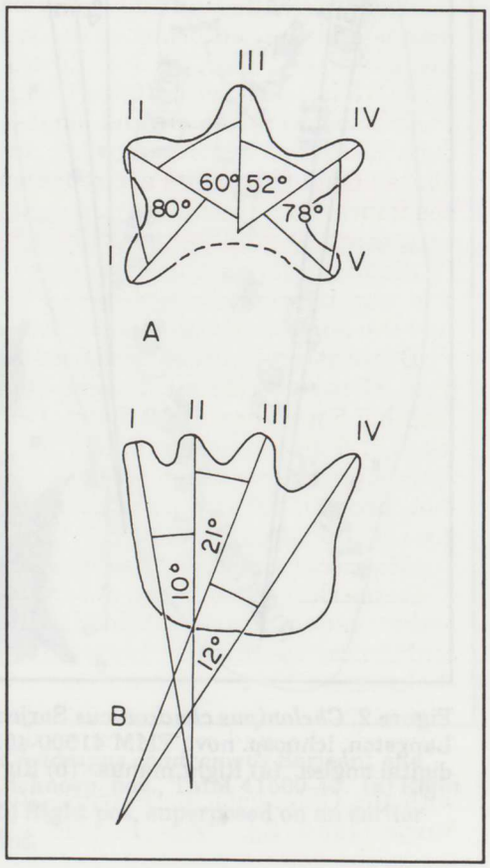


Figure 5. (Right) *Chelonipus parvus* Sarjeant and Langston, TMM 41500-23. Interdigital angles. (a) Right manus. (b) Right pes (reversal of fig. 4b, to facilitate comparison).

Chelonipus parvus
Sarjeant and Langston, ichnosp. nov.

Plate 6a-b. Figures 3-5.

Derivation of Name. Latin *parvus*, little.

Diagnosis. Quadrupedal footprints of small size, exhibiting a broad trackway and short stride. Impressions of manus directed outward, those of pes forward. Manus digitigrade, pes typically semiplantigrade or plantigrade. Manus digits short and clustered in a stellate pattern, with the pollex and digit II directed forward, digit III outward and digits IV and V backward; pes digits very short and blunt, with I-III directed forward and IV directed outward. Claws not indicated; no tail-drag impression.

Type Specimen. TMM 41500-23, on slab 41500-17 (with bird footprints).

Horizon and Locality. See Introduction.

Description. This trackway is that of a small animal walking forward and then pausing and turning. The manus impressions are digitigrade and directed outward, rather than forward; those of the pes are directed forward. None of the digits shows clear claws; rather, they are hooflike. The palm was arched over the surface, perhaps as a consequence of pushing backward with the manus to pull the heavy body forward, and left no impression.

Because of the unusual angle between the manus and the centerline of the track (fig. 3), the pollex and digit II are directed forward, digit III laterally and digits IV and V backward; the two latter are the longest and slimmest of five short, broad-based and tapering digits. Only four digits are represented in the pes impression, the hallux and digits II and III very short, blunt and forwardly directed, digit IV distinctly larger and directed outward. The sole was impressed deeply and evidently carried the animal's greatest weight.

Dimensions. Breadth of trackway 34 mm; pace 37 mm; stride ca. 40 mm. Right manus: length 8.5 mm, breadth 9.5 mm. Length of digits: I, 1.5 mm; II, 1.5 mm; III, 2.5 mm; IV, 3.0 mm; V, less than 2 mm. Left pes: length 7.5 mm, breadth 7.0 mm. Length of digits: I, 1.8 mm; II, 1.8 mm; III, 1.6 mm; IV, 2.0 mm.

Divarication of Digits. See fig. 5.

Remarks. Though the nature of the trackmaker cannot be ascertained with complete confidence, we think it likely to have been a chelonian. The broad trackway and evident awkwardness of walking, as manifested by the outwardly directed manus impressions, suggest a rather inefficient pedestrian and compare well with the Oklahoma turtle track illustrated by Murie (1954, fig. 185c). In tracks of frogs or toads, the manus is turned inward rather than outward, whereas other types of amphibians have longer digits and tend to drag their tails.

The small size is noteworthy: this may have been either a young turtle or one only attaining a small adult size.

CLASS AVES
SUBCLASS NEORNITHES

The fossil footprints of birds have been reported widely, though not frequently (for a history see Sarjeant, 1987). Bird footprints present particular problems to the paleoichnologist in that they can be used only to a limited extent to identify particular systematic categories. This is because, to an even greater degree than in other animal groups, the morphology of the foot represents behavior rather than affinity. Consequently, though the makers of some bird tracks can be named with reasonable confidence, much more often their identification is difficult or impossible.

A second consequence, and an additional problem, is that, whereas numerous texts deal with modern mammal tracks, few treat modern bird tracks and, even when they do (e.g., Teuwsen, 1920; Jaeger, 1948), the treatment is only partial. As a result, the paleoichnologist has no good basis for making comparisons.

A third consequence is that few paleoichnologists have tried to place avian ichnites into any taxonomy. Lambrecht (1938) listed the few attempts up to that date; two species were assigned to a genus shown subsequently to comprise dinosaur footprints, and others were placed in osteologically based genera.

Panin and Avram (1962) inaugurated the modern approach by distinguishing several avian footprint ichnogenera, which they in turn assembled into families. Unfortunately, their work presents several technical problems. First, it is written in Rumanian, and, though synopses in French and Russian were provided, the taxonomic sections were not translated. This contravenes the General Recommendations of the International Code of Zoological Nomenclature (Ride et al., 1985). Second, though the ichnospecies were illustrated adequately, the descriptions were scant and furnish only a slender basis for their recognition. Third, no diagnoses were provided for the families proposed; indeed, they seem to have been conceived as an ichnological shadow of the biological classification, with a family to correspond to each bird order, regardless of potential overlap in footprint morphology. Moreover, the proposed names, e.g., Ardeipedae, contravene Article 29 of the Code (Ride et al., 1985:55) because they do not have the suffix -IDAE. In our judgment,

the ichnogeneric and ichnospecific names can be considered valid, especially since ichnofossils were not embraced by zoological nomenclature at the time of Panin and Avram's work. In contrast, their families are unusable in the absence of any definition. Moreover, the ichnogenera themselves show serious morphological overlap.

Earlier, Vialov (1961) had proposed that all bird ichnites be placed into his Order Avipedia. Later (1966), in apparent ignorance of Panin and Avram's work, he recommended that all avian ichnospecies be placed into the single genus *Avipeda*. Vialov's approach was followed by Scrivner and Bottjer (1986) but is not adopted here, since we see no merit in such a lumping-together of distinctive morphotypes.

Instead, we propose that the avian footprint ichnogenera be more lucidly defined and assembled into a number of families defined only by their morphology, without implication of phyletic affinity. We prefer this approach, even though the affinity of certain ichnogenera and species might be determined with reasonable precision, because the tracks of closely related natural genera or species within the same biological families may not be so readily identifiable. For example, the order Charadriiformes contains both species with unwebbed digits (e.g., the terns) and strongly webbed digits (the gulls, auks and puffins); the latter may be identifiable to ordinal level, but the former are not. A consistent, if simplistic, morphofamilial classification is considered preferable to any uneasy hybrid between precision and vagueness. The names proposed here resemble, in many instances, those invalidly proposed by Panin and Avram (1962), but we believe our concepts to be both broader and sounder.

Accordingly, four groupings are recognized, based on the number and relative position of digits, their proportionate length, and the presence or absence of webbing impressions. However, the cautionary remarks of Covacevich and Rich (1977:6) should be borne in mind and care should be taken to distinguish webbing impressions from the effects of mud upwelling. Moreover, diagnoses and descriptions should be based only on the best preserved in any series of footprints; minor variations do not justify changes of name.

Morphofamily Gruipedidae Sarjeant and Langston, nov.

Family Ardeipedae - Panin and Avram, 1962:473, nomen nudum.

Family Gruipedae - Panin and Avram, 1962:473, nomen nudum.

Diagnosis. Avian footprints showing four digits, three of which (II to IV) are directed forward and the fourth (I) directed posteriorly, its axis either coinciding with, or at an angle to, that of digit III. Digits united or separate proximally. Webbing absent or limited to the most proximal part of the interdigital angle.

Type Genus. *Gruipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, herein.

Other Included Genera. ◊*Antarctichnus* Covacevich and Lamperein, 1970.

◊*Ardeipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, herein.

◊*Ignotornis* Mehl, 1931.

◊*Tetraornithopeda* Kordos, 1983

Ichnogenus *Gruipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, nov.

Gruipeda - Panin and Avram, 1962:465.

Emended Diagnosis. Avian footprints showing four digits, three of which (II to IV) are directed forward and large, the fourth (I) directed backward, spur-like and short. The interdigital angles between digits II and III and between digits III and IV are less than 70°. The axis of digit I does not correspond with that of digit III, the interdigital angle between digits I and II being greater than that between digits I and IV. Webbing absent.

Type Species. ◊*Gruipeda maxima* Panin and Avram, 1962, emend. Sarjeant and Langston, herein. Miocene, Rumania.

Other Included Species. ◊*Gruipeda abeli* (Lambrecht, 1938) Sarjeant and Langston, n. comb. (= *Urmiornis abeli* Lambrecht, 1938:243-244, pl. 19). Pliocene, Iran.

◊*Gruipeda becassi* (Panin and Avram, 1962) Sarjeant and Langston, n. comb. (= *Charadriipeda becassi* Panin and Avram, 1962:467, pl. 9 fig. 30). Miocene (Helvetian), Rumania.

Gruipeda calcarifera Sarjeant and Langston, herein. Late Eocene, Texas.

◊*Gruipeda disjuncta* (Panin and Avram, 1962) Sarjeant and Langston, n. comb. (= *Charadriipeda disjuncta* Panin and Avram, 1962:467-468, pl. 9 fig. 29). Miocene (Helvetian), Rumania.

◊*Gruipeda filiportatis* (Vialov, 1965) Sarjeant and Langston, n. comb. (= *Avipeda filiportatis* Vialov, 1965:121, pl. 3 fig. 15). Miocene (Burdigalian), Ukraine.

◊*Gruipeda intermedia* Panin, 1965. Miocene (Helvetian), Rumania.

◊*Gruipeda minima* (Panin and Avram, 1962) Sarjeant and Langston, n. comb. (= *Charadriipeda minima* Panin and Avram, 1962:466, pl. 8 fig. 28). Miocene (Helvetian), Rumania.

◊*Gruipeda minor* (Panin, 1965) Sarjeant and Langston, n. comb. (= *Charadriipeda minor* Panin, 1965:146, pl. 1 fig. 6; pl. 5 Figs. 7-8; fig. 2). Miocene (Helvetian), Rumania.

Remarks. In accord with our redefinition (p. 11) of the ichnogenus *Charadriipeda*, four of its five constituent species require reattribution. Though Panin and Avram (1962) and Panin (1965) were probably correct in considering these footprints to be those of a different group of birds, in general morphological characters they are inseparable from *Gruipeda* and are thus transferred to this genus.

Gruipeda embraces footprints of birds attributable to at least three different orders: the Ralliformes (Gruiformes), Charadriiformes and Ciconiiformes. *G. filiportatis*, originally placed by Vialov into the "wastebasket" avian ichnogenus *Avipeda*, was thought by him to comprise footprints of a stork (Vialov, 1966:125). *G. abeli* Lambrecht (1938), originally placed into the osteologically based genus *Urmiornis*, was considered, like *G. maxima*, to represent the footprints of a crane and can be transferred to *Gruipeda* without hesitation.

◊*Gruipeda maxima*
Panin and Avram 1962, emend. Sarjeant and Langston, nov.

Gruipeda maxima - Panin and Avram, 1962:465, pl. 7 fig. 25.

Emended Diagnosis. Avian tracks of relatively large size, exhibiting four digits, II to IV directed forward and diverging at an angle of about 65°, digit I directed backward. Digits II to IV are similar in length, with sides almost parallel for most of their length and tapering abruptly to a pointed tip. Digit I is short, spurlike and tapering; its axis is offset at a low angle to the right from that of digit III. The impressions of digits II to IV are united proximally: digit I is separate. Webbing absent.

Type Specimen. That illustrated by Panin and Avram (1962, pl. 7 fig. 25). Lodgement not stated.

Type Horizon and Locality. Miocene (Helvetian), Prisaca-Putna, Rîpa Porcului, Rumania.

Dimensions. Type specimen: overall length 172 mm, overall breadth 180 mm. Length of digits: I, less than 10 mm; II, 120 mm; III, 140 mm; IV, 105 mm.

Divarication of Digits. I-II, 123°; II-III, 56°; III-IV, 65°; IV-I, 108°. (These measurements, taken from their figure, amplify those presented by Panin and Avram.)

Remarks. This emendation enlarges considerably the brief original diagnosis and facilitates comparison with other species of the ichnogenus. It should be noted that, although contrary to Recommendation 73C of the I.C.Z.N. Rules, failure to identify the repository does not invalidate the type description, provided that the designation includes reference to an illustration of the type, as does that of Panin and Avram.

Gruipeda calcarifera
Sarjeant and Langston, ichnosp. nov.

Plate 7. Figures 6-7.

"Vogelfährte" - Bräm, 1954:413-414, fig. 5.

Derivation of Name. Latin *calcar*, spur; *fero*, to bear, with reference to the spur-like digit I.

Diagnosis. Anisodactyl avian tracks of small size, exhibiting four digits, digits II to IV directed forward and digit I backward in spur-like fashion. Digit III is longer than digits II and IV. The interdigital angles between II and III and between III and IV are approximately 55°. The angles between digits I and II and between IV and I exceed 120°, the former smaller than the latter. The impressions of digits III and IV are united proximally; those of I and II are not or are only feebly united. The impressions of digits II to IV are biconvex and moderately long, expanding from base to midpoint and thereafter converging smoothly and progressively to their point; that of digit I is much smaller and ovoidal. Trackway narrow; stride moderate to long.

Type Specimen. TMM 41500-19.

Description. The track shows that the bird halted, turned sharply and moved forward, turned again and slowed. From the evenness of footprint depth, it appears to have been an efficient pedestrian in no particular hurry.

Dimensions. Breadth of trackway 58 mm, stride 106 mm, pace 72 mm. Pes: length 26 mm, breadth 24 mm. Length of digits: I, 4.5 mm; II, 11.5 mm; III, 17.5 mm; IV, 13.5 mm.

Divarication of Digits. See fig. 7.

Remarks. These footprints compare well in size with the tracks described from the Rumanian Miocene by Panin and Avram (1962) as *Charadriipeda* (now *Gruipeda*) *becassi*. Those authors considered them to be footprints of a snipe; however, snipe footprints are much slimmer and almost straight-sided, with a much longer digit I. In general proportions of digits, these tracks compare better with the tracks of cranes reported from the Rumanian Miocene by Panin and Avram (1962), as *Gruipeda maxima*, and from the Pliocene of Iran by

Lambrecht (1983), as *Urmiornis* (now *Gruipeda*) *abeli*. *G. calcifera* differs from *G. maxima* and *G. abeli* in its much smaller size; from *G. maxima* in that its digits II to IV are fused and much thicker distally, tapering only very slightly till the tip is approached, and from *G. abeli* in that the angle between its digits II and III and between III and IV is markedly different, digit III having a compressed tip twisting inward. Both *G. maxima* and *G. abeli* are considered to be footprints of cranes. Unnamed crane tracks reported by Yoshida (1967) and Ono (1984) from the Pliocene of Japan are again much larger than the Texas tracks, with digits II and IV longer than digit III.

These footprints are probably those of a rail. Footprints figured, but not separately described, by Moussa (1968, pl. 178 fig. 5) from the Eocene of Utah may be attributable to this ichnospecies. Bird tracks figured by Bräm (1954, fig. 5), from the subalpine Molasse of Goldau, Switzerland, may also be referable to *G. calcarifera*. However, anisodactyly is the commonest foot structure among birds (Raikow, 1985).

◊Ichnogenus *Ardeipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, nov.

Ardeipeda Panin and Avram, 1962:463.

Emended Diagnosis. Avian footprints showing four digits, three (II to IV) directed forward and large, the fourth (digit I) backward and somewhat smaller. The interdigital angles between digits II and III and between digits III and IV are less than 70°. The axis of digit I corresponds, or almost corresponds, with that of digit III, the interdigital angle between digits I and II being almost equal to that between digits I and IV. Webbing absent.

Type Species. ◊*Ardeipeda egretta* Panin and Avram, 1962, emend. Sarjeant and Langston, herein. Miocene, Rumania.

Other Included Species. ◊*Ardeipeda gigantea* Panin and Avram, 1962. Miocene (Helvetian), Rumania.

◊*Ardeipeda incerta* Panin and Avram, 1962. Miocene (Helvetian), Rumania.

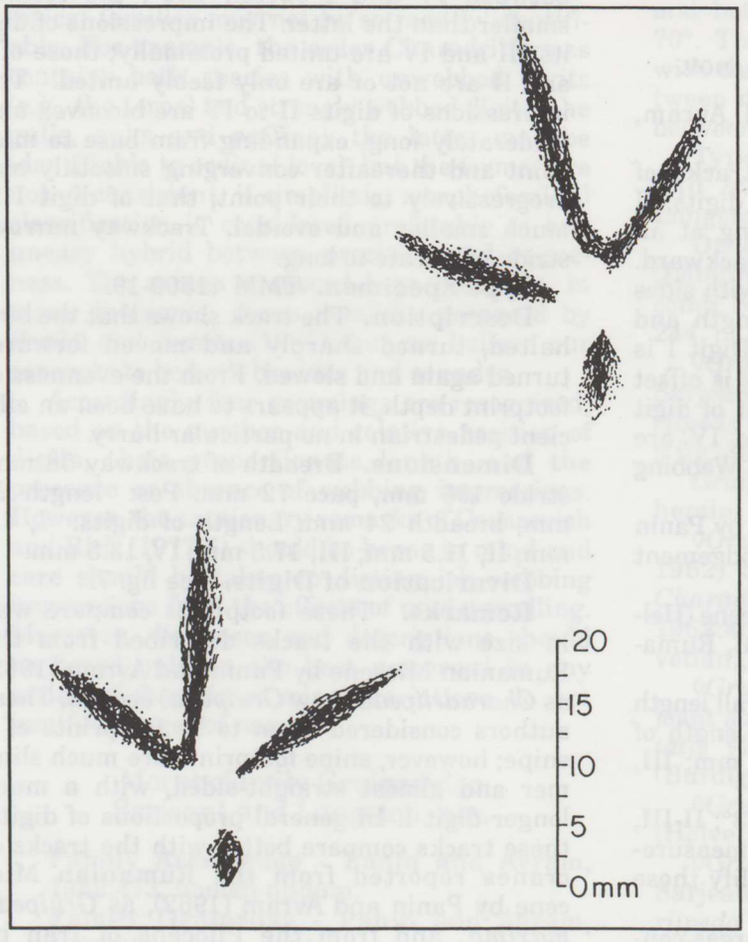


Figure 6. (Left) *Gruipeda calcarifera* Sarjeant and Langston, ichnosp. nov., TMM 41500-19. Left and right footprints.

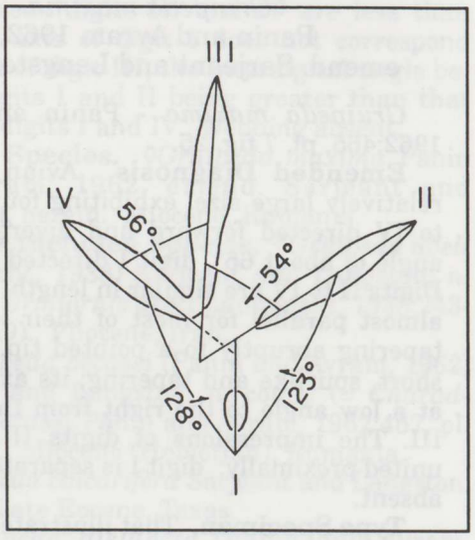


Figure 7. (Above) *Gruipeda calcarifera* Sarjeant and Langston, TMM 41500-19. Interdigital angles.

◊*Ardeipeda egretta*
Panin and Avram, 1962, emend.
Sarjeant and Langston, nov., herein.

Ardeipeda egretta - Panin and Avram, 1962:463, pl. 5 fig. 21.

Emended Diagnosis. Avian tracks of moderate size, exhibiting four digits, II to IV directed forward and I backward. All digits are slender and relatively long; digit III is longest, II and IV about four-fifths the length of digit III, digit I about three-fifths the length of digit III. Digit I forms a backward prolongation to the axis of III; the interdigital angle between digits III and IV is greater than that between digits II and III. The digits are united proximally. Trackway moderate; stride moderate.

Type Specimen. That illustrated by Panin and Avram (1962, pl. 5 fig. 21). Lodgement not stated.

Type Horizon and Locality. Miocene (Helvetian), Prisaca-Putna, Rîpa Porcului, Rumania.

Dimensions. Type material: overall length 80-85 mm, overall breadth 60-65 mm. Length of digits: I, 28 mm; II, 35-42 mm; III, 50-54 mm; IV, 38-40 mm.

Divarication of Digits. II-III, 50°; III-IV, 60°. I-II and IV-I not stated, but approximately 125°.

Remarks. This emendation amplifies the original description and serves as a more adequate basis for the ichnogeneric revision. The footprints are comparable with those of an egret.

◊Morphofamily Charadriipedidae
Sarjeant and Langston, nov.

Family Charadriipedae - Panin and Avram, 1962:473, nomen nudum.

Diagnosis. Avian footprints showing three digits, all directed forward, linked proximally and united by webbing. The webbing most often extends almost to the tips of the digits.

Type Genus. *Charadriipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, herein.

Remarks. Panin and Avram (1962) attributed four species to the ichnogenus *Charadriipeda*. The earliest listed, *C. recurvirostrioidea* Panin and Avram, is here selected as type species. It differs significantly in morphology from the other three species, all of which accord with the earlier described genus *Gruipeda* Panin and Avram; they are herein reattributed to that genus.

The family Charadriipedidae embraces webbed footprints of at least two avian orders, the Charadriiformes and Anseriformes. Though only one ichnogenus, consisting of a single species, is placed in this morphofamily, it should be noted that there are several other reports of fossil webbed avian footprints. Among these are the footprints from the Green River Shale (Eocene) of Utah described by Erickson (1967); the Lower Oligocene bird tracks reported from northern Spain by de Raaf et al. (1965); and the Pliocene (Hemphillian) tracks from the Copper Canyon Formation of Death Valley, California, described as *Avipeda* sp. E by Scrivner and Bottjer (1986).

◊Ichnogenus *Charadriipeda*
Panin and Avram, 1962,
emend. Sarjeant and Langston, nov.

Charadriipeda - Panin and Avram, 1962:465-467.

Emended Diagnosis. Avian footprints having only three digits (II-IV), directed forward and showing interdigital angles of less than 70°. Digits connected by webbing from their proximal end almost to their tips.

Type Species. ◊*Charadriipeda recurvirostrioidea* Panin and Avram, 1962, emend. Sarjeant and Langston, herein. Miocene (Helvetian), Rumania.

Remarks. This ichnogenus was originally diagnosed in vague terms, on the basis of the presumed affinity of the trackmakers rather than on its morphology. This is here corrected and, following choice of a type species, the other former constituent species have been reattributed elsewhere (see above).

◊*Charadriipeda recurvirostrioidea*
Panin and Avram, 1962,
emend. Sarjeant and Langston nov.

Charadriipeda recurvirostrioidea - Panin and Avram, 1962:465-466, pl. 7 fig. 26; pl. 8 fig. 27.

Emended Diagnosis. Avian tracks of small size, having three digits (II-IV) of unequal length, united from base almost to tip by webbing. Central digit (III) much longer than lateral digits; IV longer than II. Interdigital angle between III and IV greater than between II and III. Trackway narrow; stride moderate.

Holotype. The specimen figured by Panin and Avram (1962, pl. 7 fig. 26). Lodgement not stated.

Horizon and Locality. Miocene (Helvetian), Prusaca-Putna, Rîpa Porcului, Rumania.

Dimensions. Holotype: overall length 18 mm. Length of digits: II, 13 mm; III, 27 mm; IV, 20 mm.

Divarication of Digits. Not stated, but considered by measurement of illustrations, to be approximately II-III, 45°; III-IV, 55°.

Remarks. These footprints were considered by Panin and Avram (1962) to be those of an avocet.

Morphofamily Avipedidae Sarjeant and Langston, nov.

Diagnosis. Avian footprints showing three digits, all directed forward. Digits united or separate proximally. Webbing lacking or limited to the most proximal part of the interdigital angles.

Type Genus. *Avipeda* Vialov, 1965, emend. Sarjeant and Langston, herein.

Other Included Genera. ◊*Aquatilavipes* Currie, 1981.

◊*Aviadactyla* Kordos, 1983.

◊*Ludicharadripodiscus* Ellenberger, 1980.

◊*Fuscinapeda* Sarjeant and Langston, herein.

◊*Ornithotarnocia* Kordos, 1983.

Ichnogenus *Avipeda* Vialov, 1965, emend. Sarjeant and Langston nov.

Avipeda - Vialov, 1965:112.

Avipeda - Vialov, 1966:121.

Passeripedia Kordos, 1983 p.280,366.

Emended Diagnosis. Avian footprints of small to large size, showing three short, thick digits, with distinct claws. Length of central digit (III) less than 25% greater than that of the lateral digits. Total interdigital span 95° or less. Digits closely convergent or united proximally; webbing lacking or limited to the most proximal part of the interdigital angles.

Type Species. ◊*Avipeda phoenix* Vialov, 1965. Miocene (Burdigalian), Ukraine.

Other Included Species. *Avipeda adunca* Sarjeant and Langston, herein. Late Eocene, Texas.

◊*Avipeda ipolyensis* (Kordos, 1983) Sarjeant and Langston, comb. nov. (=*Passeripedia ipolyensis* Kordos, 1983, p. 280, 366, text-fig. 8). Lower Miocene, Hungary.

Remarks. *Avipeda* was proposed originally as a "wastebasket" genus to contain all fossil avian ichnospecies. Such an approach, though convenient, was unacceptable even at inception, since several other bird footprint ichnogenera had already been proposed (e.g., by Mehl, 1931, and Panin and Avram, 1962). Accordingly the genus is here redefined, on the basis of its type species, to embrace small, thick tridactyl footprints of birds with a short central digit and without webbing. Following this emendation, the monotypic ichnogenus *Passeripedia* Kordos, 1983, falls into synonymy. All other morphotypes have been, or should be, reallocated to other genera.

As here redefined, *Avipeda* differs from *Aquatilavipes* Currie, 1981, in the greater thickness of its digits. The *Avipeda* style of footprint is too simple to be characteristic of any particular order and even includes, at its larger end, the tracks of some ratites (e.g., the Casuariiformes and Rheiformes: see Jaeger, 1948:118).

Avipeda adunca Sarjeant and Langston, ichnosp. nov.

Plate 8b. Figures 8, 9.

Derivation of Name. Latin *aduncus*, bent inward, referring to the inwardly bent claws.

Diagnosis. Avian footprints showing three

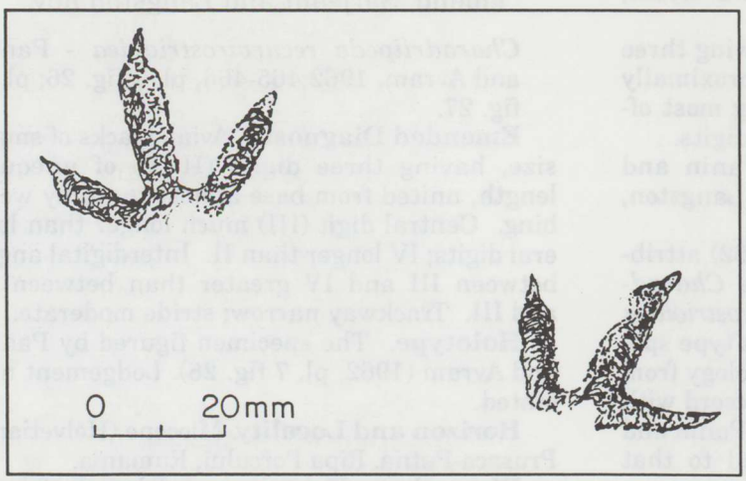


Figure 8. *Avipeda adunca* Sarjeant and Langston, ichnosp. nov., TMM 41500-24. Left and right prints made when the bird halted (at upper center in pl. 8b).

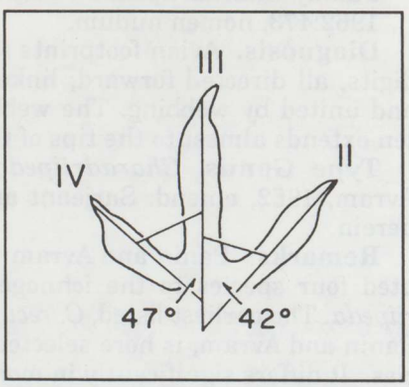


Figure 9. *Avipeda adunca* Sarjeant and Langston, TMM 41500-24. Interdigital angles.

short, relatively thick digits (II to IV), with conspicuous claws bent inward at an angle of 20 to 25° to the digital axes. Digits fused proximally. Total interdigital span less than 90°, the interdigital angle between II and III less than that between III and IV. Digit III longest; digit II about four-fifths its length, digit IV somewhat shorter. Webbing lacking. Trackway narrow; stride long.

Type Specimen. TMM 41500-24 on slab 41500-17.

Description. The track is of a bird walking forward, halting briefly, then walking forward again. The evenness of the impressions suggests it was an efficient pedestrian in no particular hurry.

Dimensions. Breadth of trackway 50 mm; stride 212 mm; pace 228 mm. Length of pes 28-30 mm, breadth 36 mm. Length of digits: II, 20 mm; III, 25.5 mm; IV, 17 mm.

Divarication of Digits. See fig. 9.

Remarks. These tracks compare well with *Avipeda phoenix* (Vialov, 1965) and *Fuscinapeda sirin* Vialov 1965, but differ from both in their more acute interdigital angle and from *F. sirin* in having a markedly shorter digit III with much shorter claws. (The lack of a "heel" to the foot—another difference—is probably a product of behavior, rather than an innate characteristic.)

Avipeda aff. *A. phoenix* Vialov, 1965

Plates 9, 14 (on right). Figures 10, 11.

Figured Specimen. TMM 41500-25 on section "D", "Grand Junction" slab (TMM 41500-22).

Description. On the "Grand Junction" slab there are several tracks of small birds, those on section D being figured here (pl. 9; fig. 10). The tracks are irregular in pattern and extent of impression, suggesting that the birds were foraging on a surface of rain-wet ash of variable moistness. Two trackways lead from bottom to top (as seen on the photograph and figure), one having been made while the surface was still moist; the detailed description is based on this. Another bird landed at about the same time and set off toward the upper right, onto drier ground. Subsequently one or more other birds landed after the surface had almost dried out. All seem to belong to the same ichnospecies—and probably to the same living species—though the later tracks are not detailed enough for complete confidence.

Fullest details are seen in three footprints, one of the right pes (pl. 9a) and two of the left pes (pl. 9b-c; fig. 11 is based on the latter). Three digits (II-IV) are impressed, the central digit slightly the longest. The interdigital angles between II and III and between III and IV are almost equal, at around 57°; the total interdigital span is thus less than 120°. All digits are thick and end in distinct claws with constricted bases and sharp points. Digit II tapers only slightly to two-thirds length, but thereafter it narrows sharply to the claw base. Digit III is thicker and does not taper until three-quarters length, when it tapers abruptly to the claw base. Digit IV tapers from slightly above base to the claw base. The three digital impressions are not linked proximally, but separate metatarsal impressions are seen in the better prints.

Dimensions. Breadth of trackway 46 mm, stride 300 mm, pace 170 mm (based on LP_2, RP_3 and LP_3 of fig. 10). Pes: overall length 34 mm, breadth 40 mm, length of digits: II, 18 mm; III, 25 mm; IV, 22.5 mm.

Divarication of Digits. See fig. 11.

Remarks. These footprints compare well to *Avipeda phoenix* from the Miocene of Ukraine. They differ only in being almost twice as large as the Ukrainian specimens. It should be noted that the interdigital angles for *A. phoenix* are not clearly defined. Moreover, Vialov's text and illustrations (1966, pl. 27-31) suggest differences between his specimens that may mean he is dealing with tracks of more than one species of bird.

◊ Ichnogenus *Fuscinapeda*
Sarjeant and Langston, nov.

Derivation of Name. Latin *fuscina*, three-pronged fork, trident; *pedis*, foot; in reference to the three prominent, clawed digits.

Diagnosis. Avian footprints of small to large size, showing three digits, slim or moderately thick (II to IV). Digit III is characteristically more than 25% longer than the lateral digits. Total interdigital span greater than 95° and often exceeds 110°. Digits united proximally, frequently showing a distinct "heel." Webbing absent or restricted to the most proximal part of the interdigital angles.

Type Species. ◊*Fuscinapeda sirin* (Vialov, 1965) Sarjeant and Langston, comb. nov. (= *Avipeda sirin* Vialov, 1965:112: see also Vialov, 1966:123, pl. 31 fig. 1) Miocene (Helvetian), Ukraine.

Other Included Species. ◊*Fuscinapeda meunieri* Sarjeant and Langston, herein. Eocene, France.

Fuscinapeda texana Sarjeant and Langston, herein. Late Eocene, Texas.

Remarks. Vialov's species is chosen as type

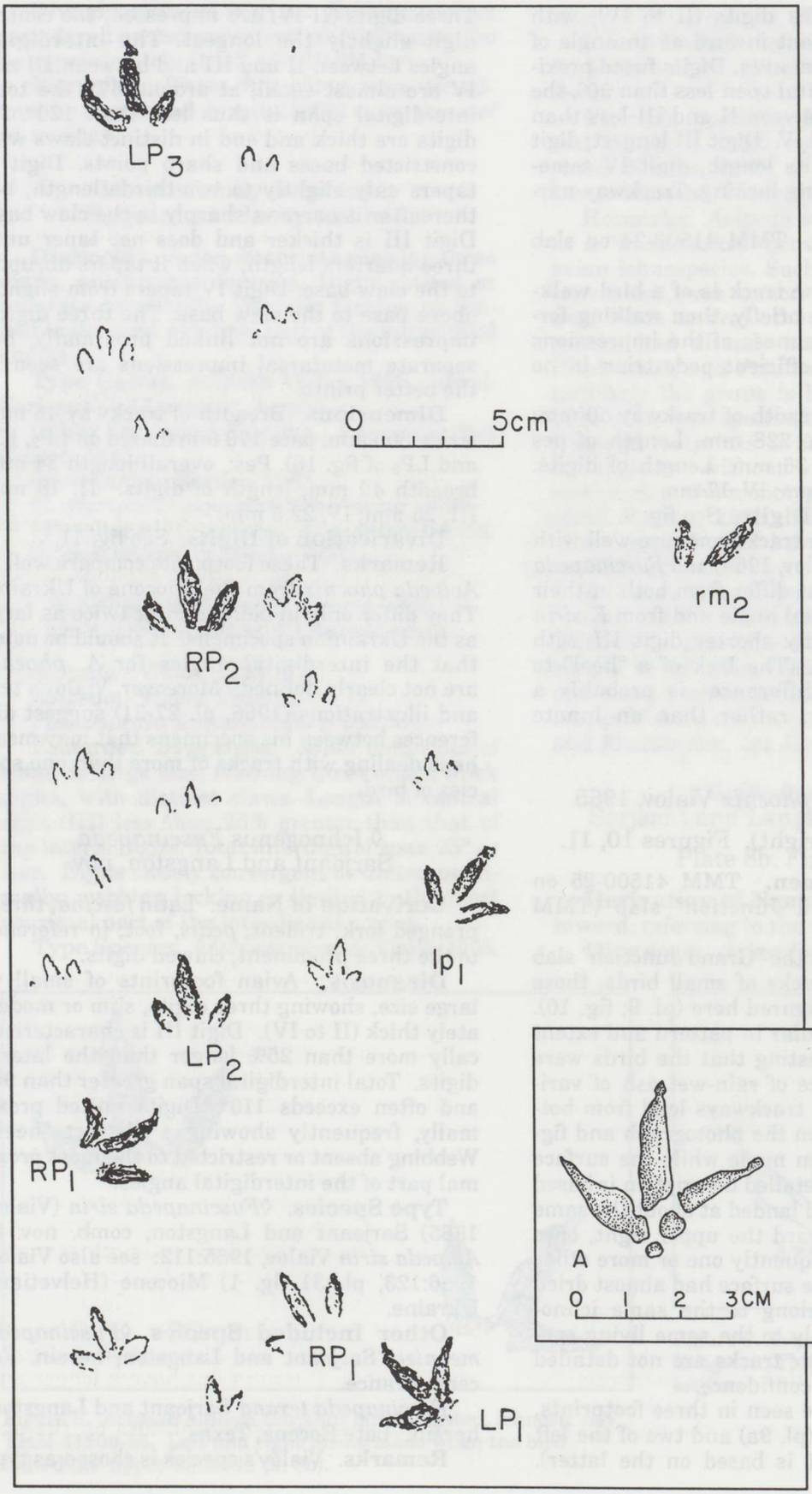


Figure 10. (Left) *Avipeda* aff. *A. phoenix* Vialov, TMM 41500-25. General drawing of the whole slab (see pl. 9). Principal track indicated by capital letters; second track by lowercase letters. The later, less clearly impressed tracks are not distinguished by letters.

Figure 11. (Below) *Avipeda* aff. *A. phoenix* Vialov, TMM 41500-25. (a) Detail of left pes (LP_1, fig. 10). (b) Divarication of digits.

since it shows both characteristic features well: a long central digit and a considerable interdigital span exceeding 110°. *T. meunieri* has a less markedly elongate central digit, while the interdigital span of *T. texana* is toward the lower end of the admissible range.

This ichnogeneric name should be applied only when the absence of any spur (digit I) can be affirmed. Incomplete impressions of Gruipedidae are easily misidentified as belonging to this genus.

Possible trackmakers include, but are not limited to, wading birds (Charadriiformes and Ciconiiformes) and, where claws are impressed, birds of prey (Falconiformes). Murie (1954, Figs. 173, 175) illustrates similar tracks made by modern birds.

The bird track illustrated as "Forma F" by Casanovas-Cladellas and Santafé-Llopis (1982, fig. 5), from the Oligocene of Agramunt (Lérida), Spain, is certainly referable to *Fuscinapeda* and merits fuller description as a fourth species of this ichnogenus.

◊*Fuscinapeda meunieri*
Sarjeant and Langston, ichnosp. nov.

"Empreintes de pas d'oiseau" - Meunier, 1906:19-21, unnumbered figure.

Derivation of Name. After the French paleontologist and stratigrapher Étienne Stanislas Meunier (1843-1925), whose description constitutes probably the earliest authentic record of fossil avian tracks.

Diagnosis. Avian footprints of moderate size, showing three digits (II to IV) of moderate thickness, with margins forming gently convex lines from base to pointed tip; claws not distinct. Central digit around 25% longer than the laterals. Total interdigital span ca. 140°; interdigital angle between digits II and III less than that between digits III and IV (ca. 65° and 75°, respectively). Webbing absent. Trackway narrow; stride moderate to long.

Type specimen. That figured by Meunier (1906:19), lodged in the Muséum National d'Histoire Naturelle, Paris, France.

Horizon and Locality. Gypsum block, Eocene, Pin, near Villevaudé (Seine-et-Marne), France.

Dimensions. Breadth of trackway 64 mm; pace 130 mm; stride not measurable. Pes: overall length 32 mm, overall breadth 45 mm. Length of digits: II, 25 mm; III, 30 mm; IV, 24 mm.

Divarication of Digits. See Diagnosis.

Remarks. In view of the great historic interest of Meunier's discovery, the high quality of his illustration and the known lodgement of the type specimen, it seems to us appropriate that his name be given belatedly to these Eocene tracks.

Meunier noted that osteological remains of several sorts of birds eligible to be the trackmakers, including curlews and herons, had been reported by Cuvier from the same Eocene gypsum deposits. However, no definite opinion concerning the trackmaker's identity was expressed. Somewhat similar tracks from the Eocene (Lutetian) of Carcassone, France were considered by Plaziat (1964) to be those of wading birds.

Fuscinapeda texana
Sarjeant and Langston, ichnosp. nov.

Plate 10a. Figures 12, 13.

Derivation of Name. After Texas, site of the footprint discovery.

Diagnosis. Avian footprints of moderate to large size, showing three digits (II to IV) of moderate thickness. Digit II expands slightly from its base to just short of midlength, then tapers to its tip; sides are convex. Digit III is around 1.5 times longer than II, tapering smoothly from base to tip but showing a slight outward flexure at midlength. Digit IV is also short; it is broader-based but otherwise similar to II. Total interdigital span around 105°; interdigital angle between II and III less than between III and IV. Webbing confined to the most proximal part of the interdigital angles. The footprints show a pronounced angular "heel." Trackway narrow; stride long.

Type Specimen. TMM 41500-26, track at position 13 on section C, "Grand Junction" slab (41500-22).

Horizon and Locality. See Introduction.

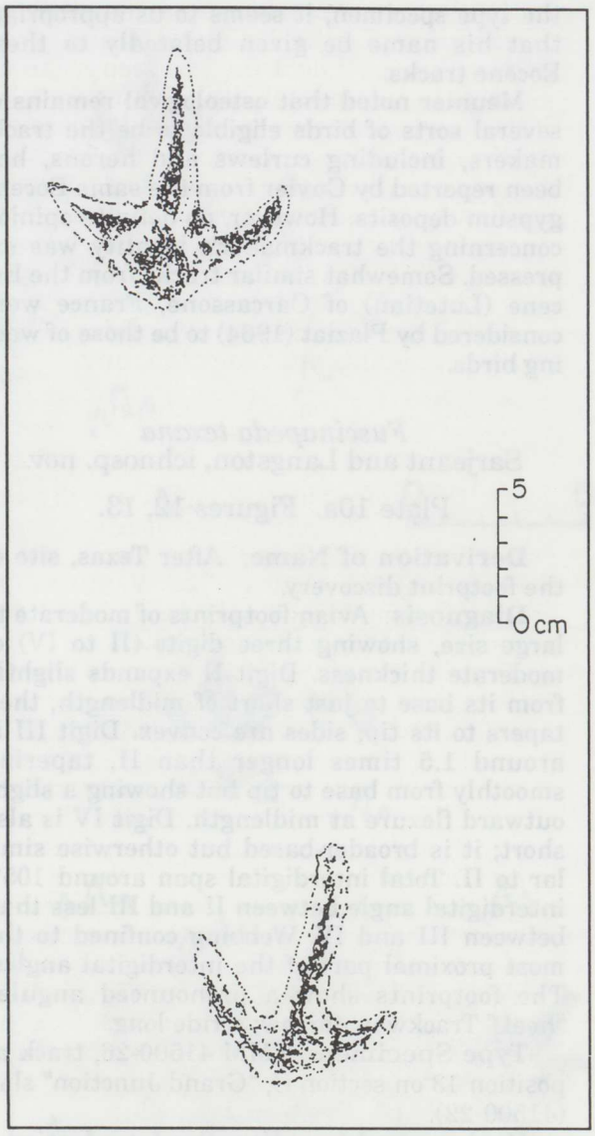
Description. A single, distinct trackway of a large bird traverses part of section C of the "Grand Junction" slab, subsequently becoming confused with other tracks but seen faintly as continuing onto section A (pl. 4). Only two footprints are clear (fig. 12); the diagnosis is based on the upper, better imprint (the right pes). Trackway narrow; stride long.

Dimensions. Breadth of trackway 99 mm; pace 223 mm; stride 557 mm. Pes: length 96-100 mm, breadth 82-86 mm. Length of digits: II, 38-40 mm; III, 70-72 mm; IV, 33-34 mm.

Divarication of Digits. See fig. 13.

Remarks. Two footprints recorded by Wetmore (1956) from the Miocene of Louisiana are similar to *T. texana* but have a longer and straighter central digit (III).

In absence of osteological data on the avifauna of Late Eocene Texas, it can be remarked



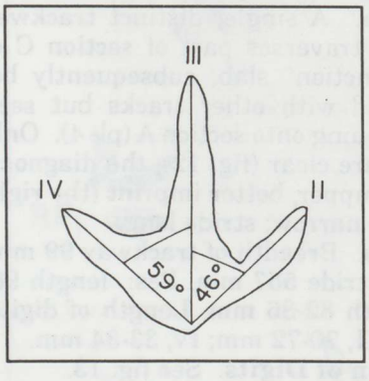


Figure 12. (Top) *Fuscinapeda texana* Sarjeant and Langston, ichnosp. nov., TMM 41500-26. Left and right prints of a walking bird.

Figure 13. (Bottom) *Fuscinapeda texana* Sarjeant and Langston, TMM 41500-26. Interdigital angles.

only that these tracks seem to be those of a large wading bird, perhaps attributable to the Ciconiiformes (herons and allies) or Charadriiformes (waders). The absence of clear claw impressions rules out any of the Falconiformes.

Fuscinapeda? sp.

Plates 11, 12b-d. Figures 14, 15.

Figured Specimen. TMM 41500-27 on the "Electric guitar" slab (41500-15). (Footprints LA_{1-2} and RA_{1-2} on key, pl. 11).

Horizon and Locality. See Introduction.

Description. A sequence of impressions of the central digit (III), or the central and outer digit (III and IV), of a large bird were impressed deeply into a surface whose extreme muddiness caused the rising of pressure ridges. The stride was very long. Digit III was around 30% longer than digit IV. Where both digits were impressed, their axes are seen to curve from a small initial interdigital angle (around 25°) through varying mutual relations—digit IV was apparently flexible—to a much larger angle (over 45°). Though the central part of the pes—the "sole"—was shallowly impressed, no trace of digit II can be seen.

Dimensions. (based on LA_1). Trackway

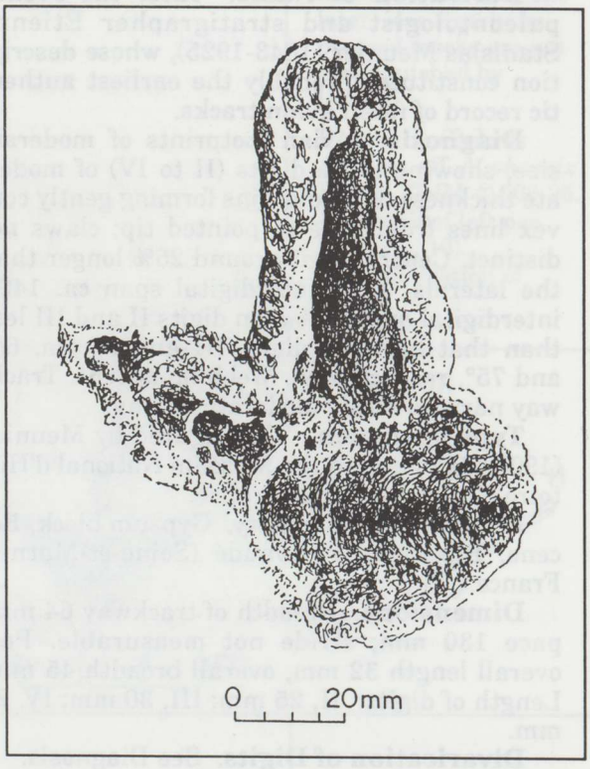


Figure 14. *Fuscinapeda?* sp., TMM 41500-27. Left pes.

breadth not measurable. Pace ca. 585 mm; stride 783 mm. Overall length of impression: 110 mm; overall breadth 75 mm. Length of digits: III, 72 mm; IV, 44 mm.

Divarication of Digits. See fig. 15.

Remarks. These imprints were made in very moist ash, of mud consistency. The wetness of the surface may be seen by comparing pl. 12d — the footprint figured in fig. 14, made on a drier surface—with pl. 12b, where the impression of digit IV is partially obliterated by back-flow of the mud. They are unusual in that no trace of digit II is seen. Even allowing for the awkward position of the feet (perhaps caused by the sticky surface), this may indicate that the foot was functionally didactyl, digit II being habitually carried clear of the ground, in lateral or posterior position.

The only existing bird exhibiting true didactyly is *Struthiocamelus*, in which digit II has been lost, but Feduccia (1980) cites probable instances in the fossil gruiform family Ergilornithidae (*Proergilornis minor*, *Ergilornis rapidus*) from the early and/or middle Oligocene of Asia. Didactyly is not known, however, in gruiforms or ratites in the New World. Three explanations for these prints thus seem possible: that they are prints of a North American ergilornithid as yet unrecognized from body fossils, that they represent a hitherto unrecognized "experiment" in didactyly by some North American gruiform group, or that they are prints of deformed *Fuscinapeda texana* feet. Favoring the last interpretation are the similar size and relative proportions of digits II and III in the two sets of tracks. The narrower divarication between digits III and IV in *Fuscinapeda* sp. might then be seen as an adjustment to reduced stability resulting from loss of the inner toe. However, the final decision on which explanation is correct must await the discovery of skeletal remains. Should either the first or the second suggestion be true, assignment of these tracks to *Fuscinapeda* will become untenable.

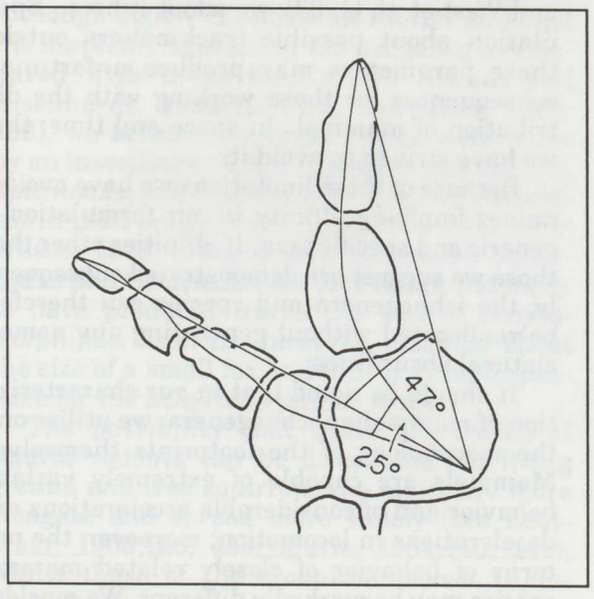


Figure 15. *Fuscinapeda?* sp., TMM 41500-27. Interdigital angles.

◊Morphofamily Anatipedidae Sarjeant and Langston, nov.

Family Anatipedae - Panin and Avram, 1962:473, nomen nudum.

Diagnosis. Avian footprints showing four digits, three of which (II to IV) are directed forward, the fourth (I) directed posteriorly, its axis either coinciding with, or at an angle to, that of digit III. Digits II to IV are united proximally and linked by webbing; digit I may be united to the others or separate.

Type Genus. ◊*Anatipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, herein.

Other Included Genus. *Phoenicopterichnum* Aramayo and Bianco, 1987.

Remarks. The presence of an impression of a fourth digit distinguishes this morphofamily. It should be noted, however, that such impressions may be present or absent in a trackway; their absence from a particular imprint does not warrant its being given a separate name.

Footprints of this nature may be made by members of the Pelecaniformes (pelicans and allies), Phoenicopteriformes (flamingos) and Anseriformes (ducks, geese, and swans).

◊Ichnogenus *Anatipeda* Panin and Avram, 1962, emend. Sarjeant and Langston, nov.

Anatipeda - Panin and Avram, 1962:467.

Emended Diagnosis. Avian footprints showing four digits, three of which (II to IV) are large and directed forward, the fourth (I) directed backward, short and spur-like. The interdigital angles between digits II and III and between digits III and IV are less than 70°. The axis of digit I does not correspond with that of digit III, the interdigital angle between digits I and II being greater than that between digits I and IV. Digits II to IV are united proximally and linked by webbing; digit I is most often separate.

Type Species. ◊*Anatipeda anas* Panin and Avram, 1962, emend. Sarjeant and Langston, herein. Miocene (Helvetian), Rumania.

Remarks. The footprints in this ichnogenus are characteristically those of ducks, geese and swans (Anseriformes).

Anatipeda anas
Panin and Avram, 1962,
emend. Sarjeant and Langston, nov.

Anatipeda anas - Panin and Avram, 1962:467, pl. 10 Figs. 31-32.
Anatipeda anas Panin and Avram-Panin, 1967:148, fig. 4.

Emended Diagnosis. Avian tracks of small to moderate size, exhibiting four digits, II to IV curving and directed forward, I directed posteriorly at an angle of about 45° to the axis of digit III. Digits II and III are of similar length, around five times as long as digit I. Digit III curves slightly, digits II and IV more strongly, digits II and III curving outward and digit IV inward. The proximal axes of these three digits have an interdigital angle of around 90°, whereas owing to their curvature they become almost parallel distally. Webbing links the digits almost to their tips. Trackway moderate; stride moderate.

Type Specimen. That illustrated by Panin and Avram, 1962, pl. 10 fig. 32. (The illustration is reproduced also in Panin, 1965, fig. 4). Lodgement not known.

Type Horizon and Locality. Miocene (Helvetian), Prisaca-Putna, Rîpa Porcului, Rumania.

Dimensions. Type specimen: length of digit I, 10 mm; length of digits II to IV, 50 mm. Range of dimensions (see Panin, 1965:148): length of digit I, 5-10 mm; digit II, 48-51 mm; digit III, 50-58 mm; digit IV, 48-51 mm.

Divarication of Digits. See Diagnosis.

Remarks. The original, very brief diagnosis was amplified somewhat by Panin (1965:148) and is greatly expanded here.

CLASS MAMMALIA

Scrivner and Bottjer (1986) have provided a succinct summary of the difficulties and potential pitfalls of mammalian ichnite analysis. Nevertheless, mammal footprints afford much more detail than bird footprints. They are often less complicated than tracks of reptiles, but correlations between soft-tissue pads and the underlying foot skeleton are frequently less exact than in the "lower" vertebrates. Moreover, the small bones of the feet are commonly lacking, even from mammals' skeletons otherwise reasonably complete; in very many fossil mammals, these bones are unknown.

Even when the relevant bones have been found, the phalangeal skeletons of fossil mammals have been given short shrift by authors who have considered them only minor interest. Moreover, while one can infer a great deal about bone structure from reptile ichnites, it is sometimes unclear how much of the underlying foot skeleton is represented by a mammalian track. For example, in digitigrade carnivores (e.g., canids and felids) the distance from the tip of a digit to the posterior edge of the sole pad usually represents only the combined lengths of the phalanges, which may be more or less extended (canids) or flexed (felids). In the absence of claw marks, it may be uncertain whether such a track belonged to one or the other of these taxonomic groups. This problem is exacerbated in the Paleogene, when some cat-like animals may have lacked retractile claws and some dog-like forms may have possessed them. Consequently it may not be possible to know, from the tracks, even whether the trackmaker had long or short toes; thus, the identification of mammal taxa based on footprints becomes more subjective in older Tertiary strata.

Given the above circumstances, the best that can usually be done with older Tertiary tracks is: 1) to infer the most likely taxonomic group by comparisons of gross ichnological features with a modern analog (if one can be found) at the lowest possible systematic level, and 2) to compare the size of the ichnites with appropriate skeletal fossils of groups present in the same, or a nearby, geographic area and at the same, or a proximate, stratigraphic level. This procedure has been followed by Bjork (1976) and West et al. (1983); we adopt it here. Speculation about possible trackmakers outside these parameters may produce unfortunate consequences for those working with the distribution of mammals in space and time; thus we have striven to avoid it.

Because of these limitations we have avoided names implying affinity in our formulation of generic and specific taxa. If affinities other than those we suggest are demonstrated subsequently, the ichnogenera and species can therefore be reallocated without generating any nomenclatural absurdities.

It should be noted that in our characterization of mammalian ichnogenera, we utilize only the morphology of the footprints themselves. Mammals are capable of extremely variable behavior and of considerable accelerations and decelerations in locomotion; moreover, the patterns of behavior of closely related mammal species may be markedly different. We consider, therefore, that stride and breadth of trackway, both controlled by pace of movement, are not

appropriate parameters for characterizing mammalian ichnogenera. We utilize them only in the characterization of ichnospecies and, even then, as identifying features very much subordinate to morphology.

All mammalian morphotypes in the ichnofauna here described appear referable to the Eutheria.

ORDER INSECTIVORA

Ichnogenus *Schyromorphipus* Sarjeant and Langston, nov.

Derivation of Name. Greek *schyros*, hedgehog; *morphe*, form, shape; *pous*, foot; with reference to the resemblance of the foot structure to that of a hedgehog.

Diagnosis. Small, plantigrade mammalian footprints; all digits with claws. Pes somewhat larger than manus. Manual digits II to V are thick and short, diverging from one another only at small angles, their total interdigital span not exceeding 35°. The pollex is set behind them. It is markedly shorter than digits II to V, diverging from the axis of the manus at an angle of around 25°. Palm proportionately long. Digits II to V of the pes are similar to those of the manus; the hallux is much shorter than the other digits but diverges at a lower angle (<15°) than does the pollex. Heel long.

Type Species. *Schyromorphipus oxypages* Sarjeant and Langston, herein. Late Eocene (Chadronian), Texas.

Remarks. These Texas tracks suggest a foot structure strikingly like that of the European hedgehog (*Erinaceus europaeus* Linnaeus). Although digit V is somewhat shorter and digit I is markedly opposed in the hedgehog as compared with these tracks (see Brandt and Eisenhardt, 1922:128-131; Leutscher, 1960: 139), we believe the Texas tracks were made by an insectivore. Three insectivores, *Leptictis*, *Apternodus*, and *Centetodon* (=*Geolabis*) are present in the Porvenir local fauna (Novacek, 1976; Wilson, 1978; Lillegraven et al., 1981). *Apternodus* and *Centetodon* are tiny forms, not likely to have produced tracks the size of *Schyromorphipus*. *Leptictis*, however, attained about the size of a small fox and thus may be responsible for the *Schyromorphipus* tracks.

The possibility that these are tracks of sciurid rodents can be discounted. In living ground and tree squirrels, the digits are more elongate and spread more widely (see Leutscher, 1960:128, 134; Murie, 1954:140, 142), whilst those of the mountain beaver (*Aplodontia*), most primitive of living rodents, are more elongate and almost parallel (see Murie, 1954:128,188).

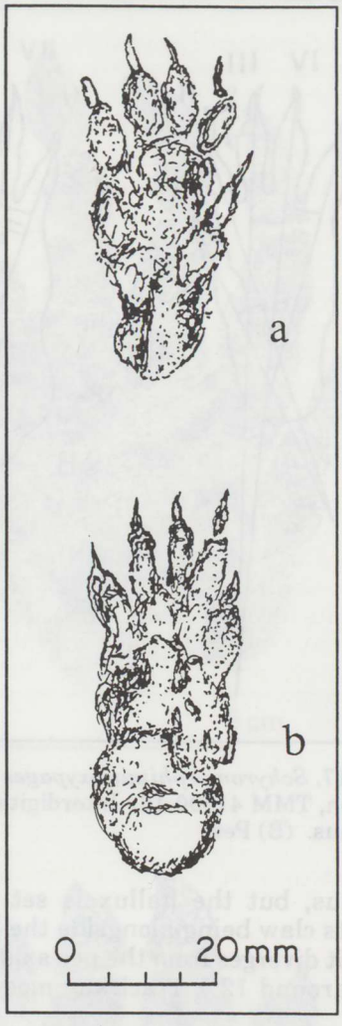


Figure 16. *Schyromorphipus oxypages* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-16. (a) Left manus. (b) Left pes.

Schyromorphipus oxypages Sarjeant and Langston, ichnosp. nov.

Plate 13. Figures 16, 17.

Derivation of Name. Greek *oxypages*, sharp-pointed; in reference to the sharp claws.

Diagnosis. Small, plantigrade mammalian footprints, with pes somewhat larger than manus and heel proportionately somewhat broader than palm. All digits bear sharp, narrow claws. Manual digits thick, with convex margins, and short (slightly over one-third the length of the palm). Digits II to V are directed forward, diverging from one another at such slight angles that their total interdigital span is less than 40°. The pollex is set behind them, the tip of its claw scarcely reaching to the base of digit II; it diverges from the manus axis at around 25°. The digits of the pes are similar to those

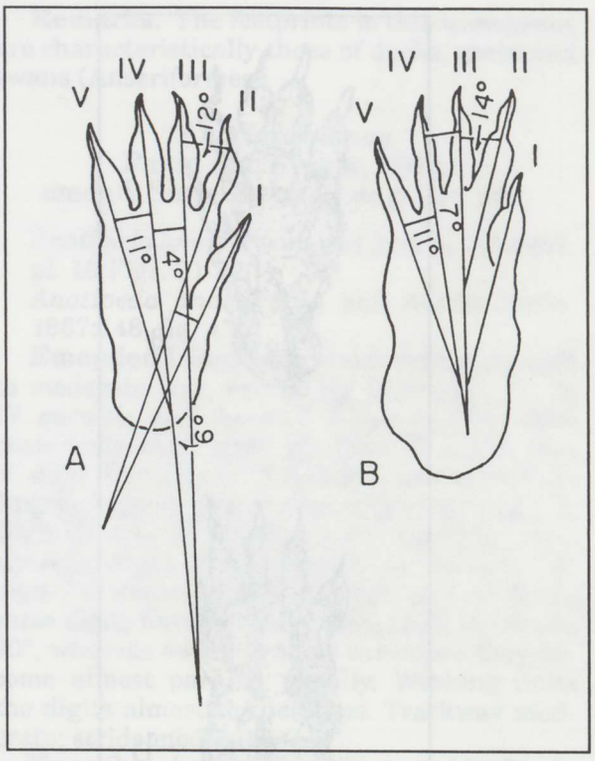


Figure 17. *Schyromorphipus oxypages* Sarjeant and Langston, TMM 41500-16. Interdigital angles. (A) Manus. (B) Pes.

of manus, but the hallux is set further forward, its claw being alongside the base of digit II, and it diverges from the pes axis at a smaller angle (around 12°). Trackway moderate; stride long.

Type Specimen. TMM 41500-16.

Horizon and Locality. See Introduction.

Description. The trackway shows six successive footprints, two of the fore feet and four of the hind feet, of a fox-size animal traveling across a surface sufficiently moist for its small weight to create pressure mounds around the prints. The impressions show the front part of the carpus and tarsus, suggesting that the animal traveled in a half-crouch; nevertheless, their spacing indicates a habitual pedestrian, rather long-bodied, ambling along steadily but without haste.

Dimensions. Breadth of trackway: 81.5 mm; pace 203.5 mm; stride 359 mm. Manus: overall length 48 mm, overall breadth 22 mm. Length of digits: I, 12 mm; II, curved, 15 mm; III, 14 mm; IV, 14.5 mm; V, 13.5 mm. Pes: overall length 54 mm: overall breadth 21 mm. Length of digits: I, 14 mm; II, 15 mm; III, 14 mm; IV, 14 mm; V, 12 mm.

Divarication of Digits. See fig. 17.

Remarks. For discussion of affinities, see under genus.

ORDER CREODONTA

Ichnogenus *Zanclonychopus*, Sarjeant and Langston, nov.

Derivation of Name. Greek *zanclos*, sickle; *onychos*, claw; *pous*, foot; with reference to the curving claws.

Diagnosis. Plantigrade footprints, with manus and pes of similar size and with all digits strongly clawed. Digits II to IV most deeply impressed and forming, with palm or sole, an approximately oval shape (more marked in the pes); digit I set off to one side and impressed lightly or not at all. Tips and claws of inner digits curving outward, of outer digits curving inward. Inner phalangeal pads of pes fused; those of manus free.

Type Species. *Zanclonychopus cinicalcator* Sarjeant and Langston, herein. Late Eocene (Chadronian), Texas.

Remarks. Two trackways, representing individuals of different size, are apparently attributable to one species of creodont. Using the formula for ascertaining gleno-acetabular length (BL) proposed by Demathieu, 1970 (see Leonardi, 1987), for an ambling mammal with upright limbs (BL = one hand-foot distance + stride length) we obtain a value of 1665 mm for the larger *Zanclonychopus* individual. The apparent limb length thus ranges from 1150 mm to 1665 mm, depending on the assumed stride angle of 30° to 60°, respectively—the range for existing mammals (Demathieu, in Leonardi, 1987). The lower value is more likely, because of the apparently somewhat lumbering progression of the animal suggested by what, for a mobile quadruped, is a relatively wide trackway (2.5 times the width of the pes).

These highly subjective dimensions indicate an animal within the size range of the American black bear (*Ursus americanus*), which has an average head-to-rump length of ca. 1675 mm and a shoulder height of 760 mm. How closely the animal resembled a bear is, of course, conjectural, but the substantially smaller paw prints of *Zanclonychopus* suggest that this animal was less robust than a black bear.

Certainly the *Zanclonychopus* tracks appear to be those of a large plantigrade mammal with mesaxonic feet. These features rule out most unguiculate mammals except a few archaic groups, including the Creodonta (sensu Mellet, 1977). If they were made by a creodont, the size of the prints (within the range of a mountain lion, *Felis concolor*) suggests hyaenodont affinities.

Tracks from the late Eocene of Garrigues-Ste.-Eulalie (Gard), France, ascribed by Ellen-

berger (1980) to an hyaenodont, are comparable to those here described; they both have an ovoid outline, with one laterally placed digit. However, the proportions and curvature of both manual and pedal digits are different. Although the French tracks do not furnish such clear details as those from Texas, they reflect a quite dissimilar pattern of pedal digits, with II to IV directed forward and V, as well as I, laterally.

Other possible creodont tracks have been reported from the latest Eocene of west Texas under the ichnogeneric name *Dischidodactylus* Sarjeant and Wilson (1988), but they are so unusual in character that their attribution to a creodont seems no more reasonable than to the Insectivora.

The Porvenir local fauna contains three hyaenodontids (Gustafson, 1986): *Hyaenodon* (*Neohyaenodon*), *Hemipsalodon*, and the problematic *Ischnognathus*. Although *Zanclonychopus* tracks fall within the expected size range of *Hyaenodon* species, *Hyaenodon* had digitigrade feet and must therefore be excluded. *Ischnognathus* is so imperfectly known that it scarcely merits speculation. The feet of *Hemipsalodon* are not known but, to judge from the skull of *H. viejensis*, that species may have been of the appropriate size to be the trackmaker.

Zanclonychopus cinicalcator
Sarjeant and Langston, ichnosp. nov.

Plates 14, 15. Figures 18, 19a, 20.

Derivation of Name. Latin *cinis*, ashes; *calcator*, one who treads something; thus "ash-treader," in reference to the circumstance of formation of these footprints.

Diagnosis. Plantigrade footprints of moderately large size, each digit bearing a pointed claw. Manus and pes of approximately equal size; manus and manual digits more slender and flexible than pes and pedal digits. Digits I to III of both manus and pes curve slightly outward, digits IV and V slightly inward. Digits II to IV, together with the palm and sole, form an elongate oval shape (more obvious in the pes) and are deeply impressed. The pollex and hallux are smaller than the other digits of their respective feet, the pollex being markedly more slender and somewhat separate, the hallux even slenderer; they are very lightly impressed even on soft substrates and unlikely to be visible at all on harder substrates. The proximal phalanges of digits II to IV of the manus are separate, whereas those of the pes are fused with the sole, so that the free length of the pedal digits is much less than that of the manual digits. Trackway moderate; stride long.

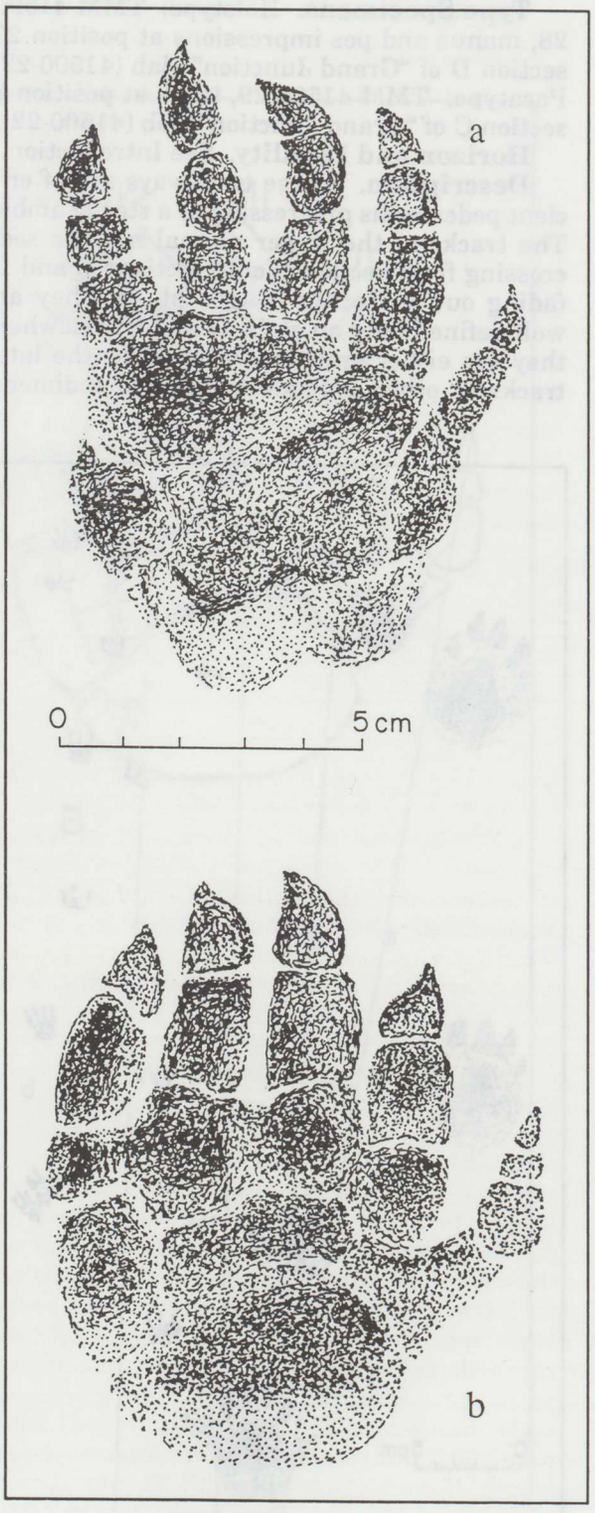


Figure 18. *Zanclonychopus cinicalcator* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-28. (a) Left manus. (b) Left pes.

Type Specimens. Holotype: TMM 41500-28, manus and pes impressions at position 27, section D of "Grand Junction" slab (41500-22). Paratype: TMM 41500-29, track at position 8, section C of "Grand Junction" slab (41500-22).

Horizon and Locality. See Introduction.

Description. These trackways are of efficient pedestrians progressing at a steady amble. The tracks of the larger animal may be seen crossing from section F onto sections E and D, fading out on section C (see pl. 4). They are well defined only on slabs D and C; elsewhere they are either much overprinted by the later tracks of other animals or are too sediment-filled for study. The second trackway, of a smaller animal here designated as paratype, begins on "Grand Junction" section B but is well seen only on section C, which is traversed across its greatest width. Unfortunately, because of cracking and flaking of the surface, only two manus and two pes prints are relatively clear.

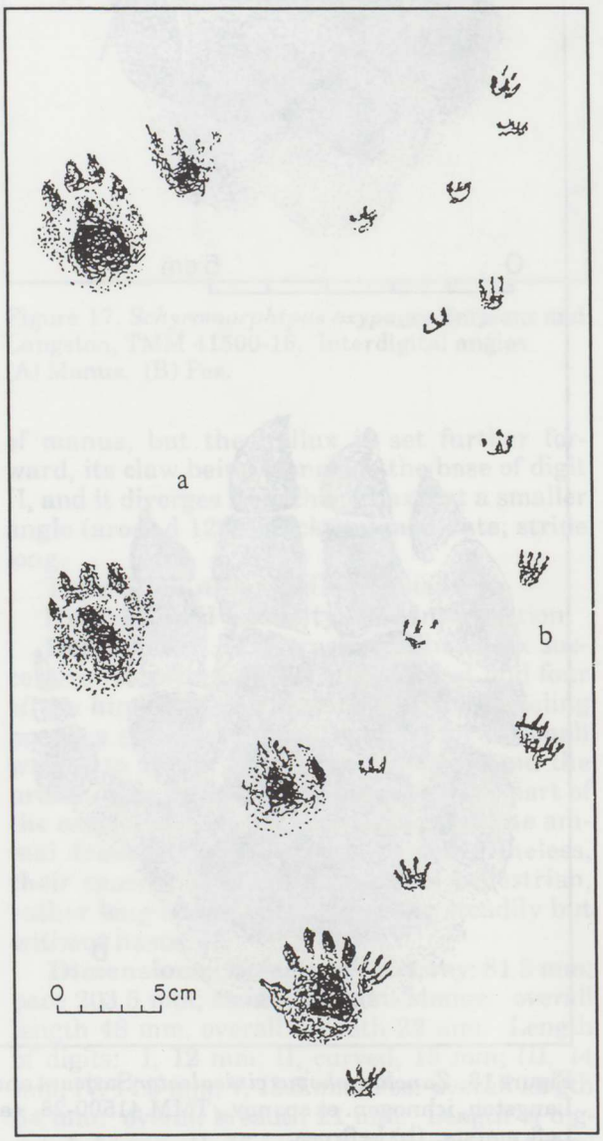


Figure 19. (a) Tracks of a smaller specimen of *Zanclonychopus cinicalcator* Sarjeant and Langston (TMM 41500-29). (b) Rodent tracks of Type A (TMM 41500-39), probably a sciuromorph.

Dimensions. Holotype: breadth of trackway ca. 205 mm; pace 1150 mm; stride 1575 mm. Manus: overall length 107 mm, maximum span of digits 77 mm. Length of digits: I, 26 mm; II, 43 mm; III, 43 mm; IV, 44 mm; V, 37 mm. Pes: overall length 98 mm, maximum span of digits 84 mm. Length of digits: I, 36 mm; II, 30 mm; III, 36 mm; IV, 34 mm; V, 35 mm. (Note: The disproportionate apparent length of the hallux, actually the smallest digit, results only from the fact that it is free proximally, whereas the others are not, so that their proximal phalanges are not included in the measurement). Paratype: Breadth of trackway 84 mm; pace 161 mm; stride 312 mm. Manus: overall length 32 mm, maximum span of digits 41 mm. Length of digits: I, ca. 12 mm; II, 9 mm; III, 8 mm; IV, 8 mm; V, 9 mm. (Based on several impressions, none being ideal). Pes: overall length 34 mm, overall breadth 25 mm. Length of digits: I, 7 mm; II, 8 mm; III, 8 mm; IV, 7 mm; V, 5 mm.

Divarication of Digits. Taken from the holotype. Since the digits curve so markedly, positions of measurement are arbitrary and shown on fig. 20. Left manus: I to II at base 20°, near tip 43°; II to III at base 7°, near tip 25°; III to IV at base 11°, tips convergent; IV to V at base 5°, near tip 26°. Left pes: I to II at base 41°, near tip 6°; II to III, at base nearly parallel, near tip 27°; III to IV at base parallel, near tip 20°; IV to V at base 25°, tips convergent. (It should be stressed that the manual digits were quite flexible, so that readings of interdigital angles on other imprints are sharply different. In contrast, the pedal digits were more rigid, the interdigital angles between the four larger digits showing virtually no variation.)

Remarks. There is a great disparity in size between the two tracks. The maker of the smaller (paratype) tracks was evidently a juvenile, in whose footprints the indications of digits—either because of the circumstances of their impression, or because the individual weighed less—were less distinct than in the adult. The two sets of tracks must have been made at about the same time, because both have tracks of other animals superimposed upon them. It is tempting, therefore, to think the two animals may have been dam and cub.

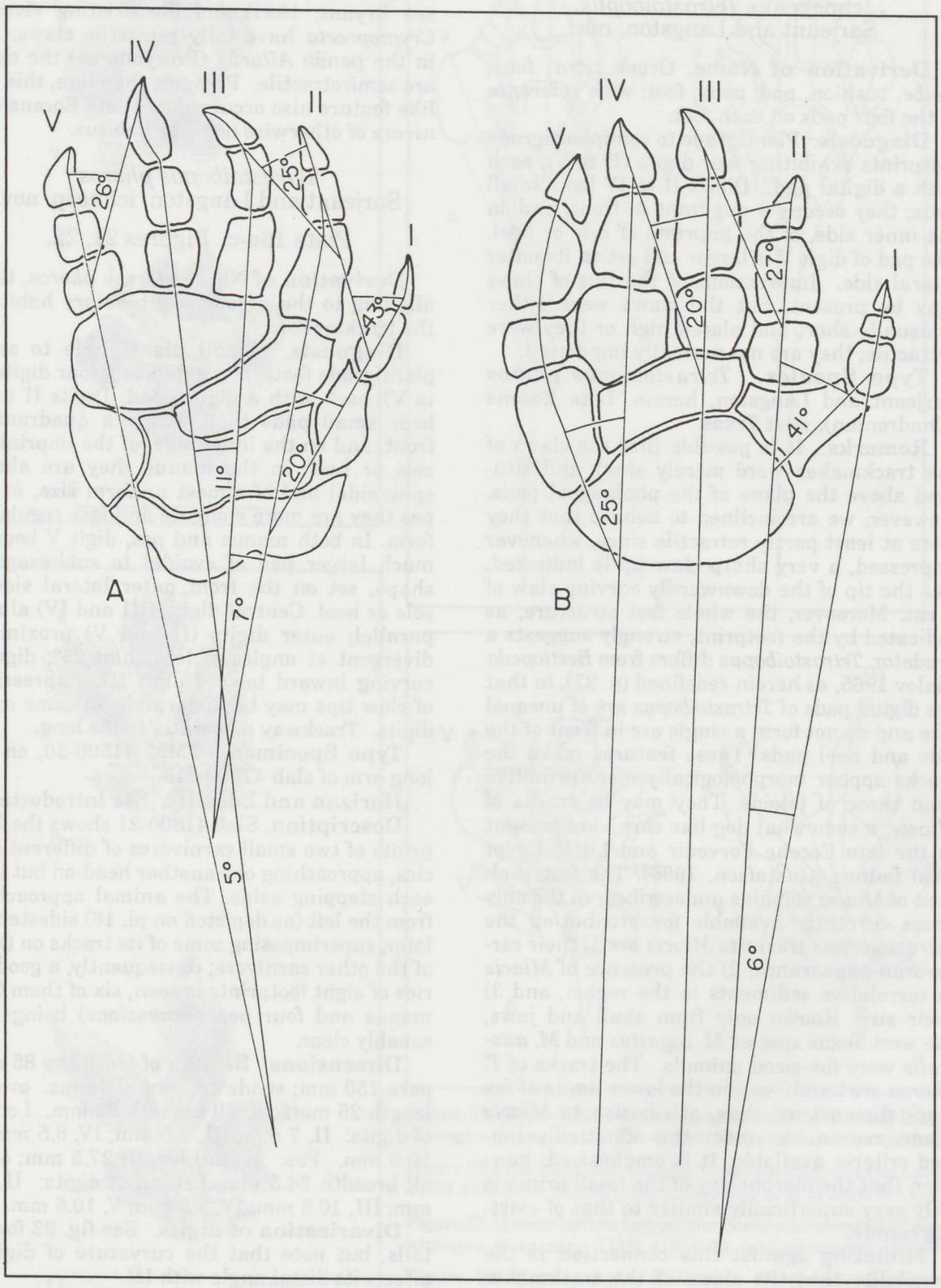


Figure 20. *Zanclonychopus cinicalcator* Sarjeant and Langston (TMM 41500-28). Interdigital angles. (A) Left manus. (B) Left pes.

ORDER CARNIVORA

SUPERFAMILY MIACOIDEA

Ichnogenus *Tetrastoibopus*, Sarjeant and Langston, nov.

Derivation of Name. Greek *tetra*, four; *stoibe*, cushion, pad; *pous*, foot; with reference to the four pads on each foot.

Diagnosis. Plantigrade to semiplantigrade footprints exhibiting four digits (II to V), each with a digital pad. Digits II to IV bear small pads; they occupy a quadrant in front, and on the inner side, of the imprints of sole or heel. The pad of digit V is larger and set on its outer lateral side. Impressions of the tips of claws may be present, but the claws were either unusually short and placed high or they were retractile; they are not normally impressed.

Type Species. *Tetrastoibopus phoros* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. It is possible that the claws of the trackmaker were merely short and situated above the plane of the phalangeal pads. However, we are inclined to believe that they were at least partly retractile since, whenever impressed, a very sharp claw tip is indicated, like the tip of the downwardly curving claw of a cat. Moreover, the whole foot structure, as indicated by the footprint, strongly suggests a predator. *Tetrastoibopus* differs from *Bestiopeda* Vialov 1965, as herein redefined (p. 27), in that the digital pads of *Tetrastoibopus* are of unequal size and do not form a single arc in front of the sole and heel pads. These features make the tracks appear morphologically more primitive than those of feloids. They may be tracks of *Miacis*, a somewhat dog-like carnivore present in the late Eocene Porvenir and Little Egypt local faunas (Gustafson, 1986). The foot skeleton of *Miacis* remains undescribed, so the only bases currently available for attributing the *Tetrastoibopus* tracks to *Miacis* are 1) their carnivoran appearance, 2) the presence of *Miacis* in correlative sediments in the region, and 3) their size. Known only from skull and jaws, the west Texas species *M. cognitus* and *M. australis* were fox-sized animals. The tracks of *T. phoros* are barely within the lower limits of fox track dimensions; thus, attribution to *Miacis* seems reasonable under the admittedly limited criteria available. It is emphasized, however, that the morphology of the fossil prints is only very superficially similar to that of existing canids.

Militating against this connection is the possibility that the claws of the trackmaker were retractile, a quality generally associated with cats rather than with canids. However, the feliform Nimravidae (which are not felids, but possibly the sister group of the Aeluroidea—see Bryant, 1991) and the existing viverrid *Cryptoprocta* have fully retractile claws, and in the panda *Ailurus* (Procyonidae) the claws are semiretractile. Perhaps, therefore, this catlike feature also occurred in a late Eocene carnivore of otherwise dog-like habitus.

Tetrastoibopus phoros Sarjeant and Langston, ichnosp. nov.

Plate 16a-c. Figures 21, 22.

Derivation of Name. Greek *phoros*, thief; alluding to the presumed predatory habits of the trackmaker.

Diagnosis. Small plantigrade to semiplantigrade footprints exhibiting four digits (II to V), each with a digital pad. Digits II to IV bear small pads that occupy a quadrant in front, and on the inner side, of the imprints of sole or heel; in the manus they are almost spheroidal and of almost uniform size, in the pes they are more elongate and less regular in form. In both manus and pes, digit V bears a much larger pad of ovoidal to subhexagonal shape, set on the front outer lateral side of sole or heel. Central digits (III and IV) almost parallel; outer digits (II and V) proximally divergent at angles of less than 25°; digit II curving inward toward digit III. Impressions of claw tips may be discernible on some or all digits. Trackway moderate; stride long.

Type Specimen. TMM 41500-30, on the long arm of slab 41500-21.

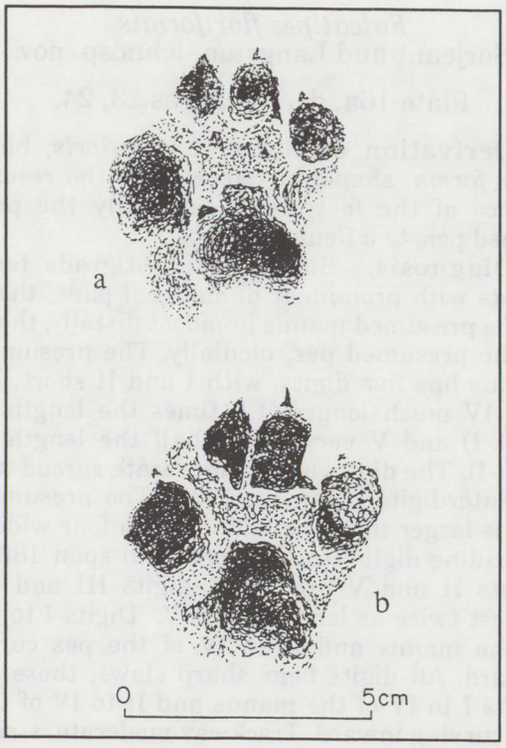
Horizon and Locality. See Introduction.

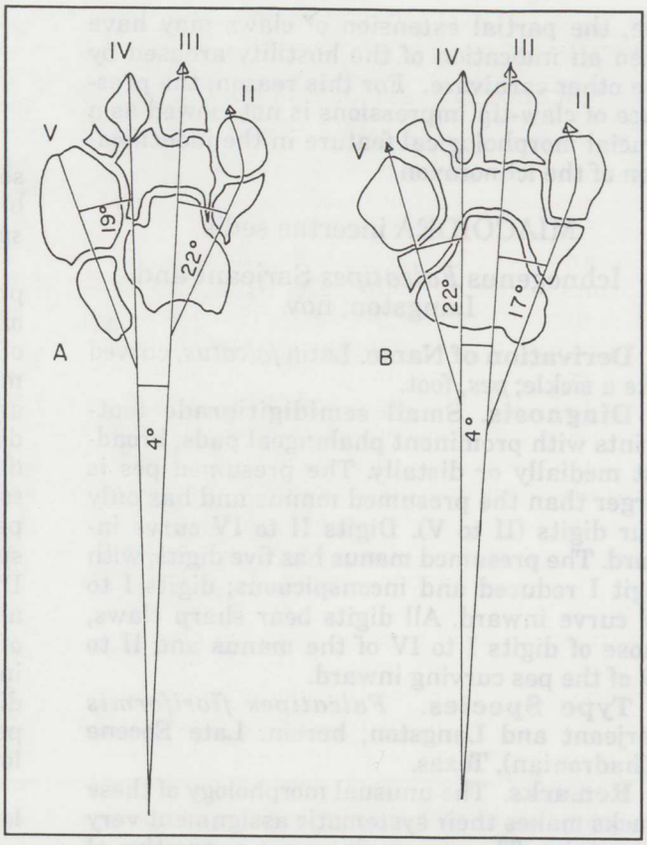
Description. Slab 41500-21 shows the footprints of two small carnivores of different species, approaching one another head-on but then each stepping aside. The animal approaching from the left (as depicted on pl. 16) sidestepped later, superimposing some of its tracks on those of the other carnivore; consequently, a good series of eight footprints is seen, six of them (two manus and four pes impressions) being reasonably clear.

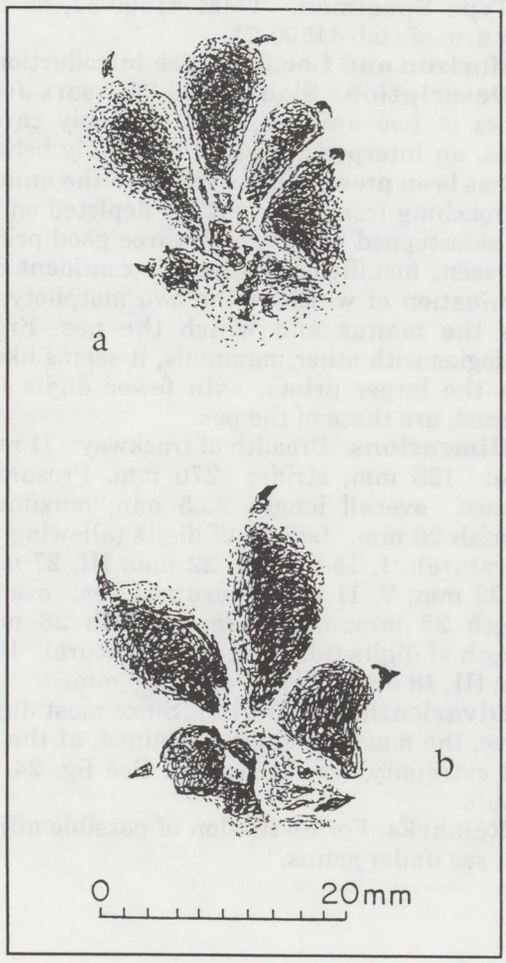
Dimensions. Breadth of trackway 85 mm; pace 150 mm; stride 482 mm. Manus: overall length 26 mm; overall breadth 22 mm. Length of digits: II, 7 mm; III, 7.5 mm; IV, 6.5 mm; V, 10.5 mm. Pes: overall length 27.5 mm; overall breadth 24.5 mm. Length of digits: II, 7.5 mm; III, 10.5 mm; IV, 8.5 mm; V, 10.5 mm.

Divarication of digits. See fig. 22 for details, but note that the curvature of digit II affects its distal angle with III.

Remarks. If indeed the claws were retrac-







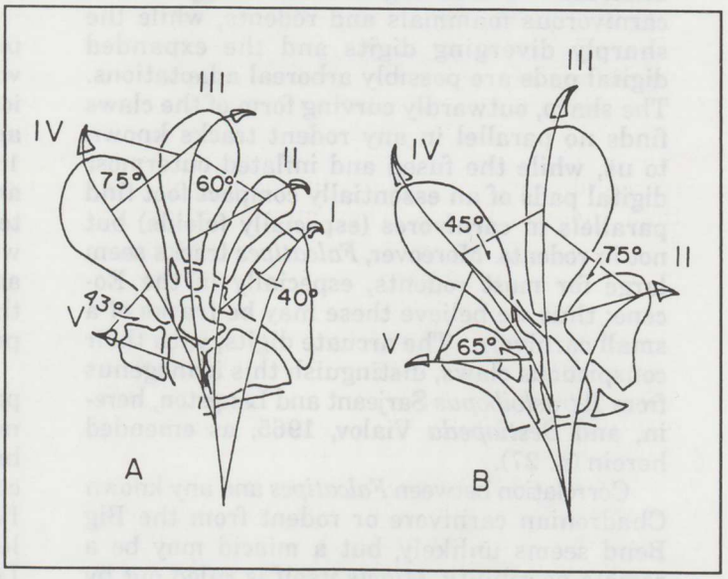


Figure 21. (Top left) *Tetrastoibopus phoros* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-30. (a) Left manus. (b) Left pes.

Figure 22. (Top right) *Tetrastoibopus phoros* Sarjeant and Langston, TMM 41500-30. Interdigital angles. (A) Left manus. (B) Left pes.

Figure 23. (Lower left) *Falcatipes floriformis* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-31. (a) Left manus. (b) Left pes.

Figure 24. (Lower right) *Falcatipes floriformis* Sarjeant and Langston, TMM 41500-31. Interdigital angles. (A) Left manus. (B) Left pes.

tile, the partial extension of claws may have been an indication of the hostility aroused by the other carnivore. For this reason, the presence of claw-tip impressions is not viewed as a crucial morphological feature in the identification of the ichnotaxon.

MIACOIDEA incertae sedis

Ichnogenus *Falcatipes* Sarjeant and Langston, nov.

Derivation of Name. Latin *falcatus*, curved like a sickle; *pes*, foot.

Diagnosis. Small semidigitigrade footprints with prominent phalangeal pads, broadest medially or distally. The presumed pes is larger than the presumed manus and has only four digits (II to V). Digits II to IV curve inward. The presumed manus has five digits, with digit I reduced and inconspicuous; digits I to IV curve inward. All digits bear sharp claws, those of digits I to IV of the manus and II to IV of the pes curving inward.

Type Species. *Falcatipes floriformis* Sarjeant and Langston, herein. Late Eocene (Chadronian), Texas.

Remarks. The unusual morphology of these tracks makes their systematic assignment very uncertain. The strong claws are suggestive of carnivorous mammals and rodents, while the sharply diverging digits and the expanded digital pads are possibly arboreal adaptations. The sharp, outwardly curving form of the claws finds no parallel in any rodent tracks known to us, while the fused and inflated outermost digital pads of an essentially compact foot find parallels in carnivores (especially feloids) but not in rodents. Moreover, *Falcatipes* tracks seem large for most rodents, especially in the Eocene; thus we believe these may be tracks of a small carnivore. The arcuate digits, with their conspicuous claws, distinguish this ichnogenus from *Tetrastoibopus* Sarjeant and Langston, herein, and *Bestiopeda* Vialov, 1965, as emended herein (p. 27).

Correlation between *Falcatipes* and any known Chadronian carnivore or rodent from the Big Bend seems unlikely, but a miacid may be a remote possibility. *Miacis* itself is ruled out by its dog-like habitus, but some other miacids may well have been arboreal, by analogy with living carnivores of comparable morphology. Unfortunately, the available trackway is too short to tell whether the trackmaker was long-bodied.

Falcatipes floriformis Sarjeant and Langston, ichnosp. nov.

Plate 16a, d, e. Figures 23, 24.

Derivation of Name. Latin *floris*, blossom; *forma*, shape; in reference to the resemblance of the footprints, especially the presumed pes, to a fleur-de-lys.

Diagnosis. Small semidigitigrade footprints with prominent phalangeal pads, those of the presumed manus broadest distally, those of the presumed pes, medially. The presumed manus has five digits, with I and II short, III and IV much longer (1.5 times the length of digit I) and V very short (half the length of digit I). The digits have a moderate spread (total interdigital span ca. 120°). The presumed pes is larger than the manus, with four widely spreading digits (total interdigital span 180°). Digits II and V are short, digits III and IV almost twice as long as II or V. Digits I to IV of the manus and II to IV of the pes curve inward. All digits bear sharp claws, those on digits I to IV of the manus and II to IV of the pes curving inward. Trackway moderate; stride long.

Type Specimen. TMM 41500-31, on the long arm of slab 41500-21.

Horizon and Locality. See Introduction.

Description. Slab 41500-21 bears footprints of two animals, both probably carnivores; an interpretation of their likely behavior has been presented above. Since the animal approaching from the right (as depicted on pl. 16) sidestepped earlier, only three good prints are seen, insufficient to permit confident determination of which of the two morphotypes was the manus and which the pes. From analogies with other mammals, it seems likely that the larger prints, with fewer digits impressed, are those of the pes.

Dimensions. Breadth of trackway: 71 mm; pace: 128 mm; stride: 270 mm. Presumed manus: overall length 23.5 mm; maximum breadth 20 mm. Length of digits (allowing for curvature): I, 18 mm; II, 22 mm; III, 27 mm; IV, 32 mm; V, 11 mm. Presumed pes: overall length 27 mm; maximum breadth 26 mm. Length of digits (allowing for curvature): II, 9 mm; III, 18.5 mm; IV, 17 mm; V, 8 mm.

Divarication of Digits. Since most digits curve, the maximum angle attained, at the distal extremity, was measured. See fig. 24 for details.

Remarks. For discussion of possible affinities, see under genus.

INFRAORDER AELUROIDEA

Ichnogenus ◊*Bestiopeda* Vialov, 1965, emend. nov.

Bestiopeda - Vialov, 1965:112.
Bestiopeda - Vialov, 1966:128.
Pumaeichnium - Aramayo and Bianco, 1987:534.

Emended Diagnosis. Plantigrade to semiplantigrade footprints exhibiting four digits (II to V), each with a spheroidal to ovoidal or elongate digital pad forming a semicircle in front of, or about the front portion of, sole or heel pads. Digital pads are of equal or similar size. Impressions of claw tips may be present, but are usually absent.

Type Species. ◊*Bestiopeda bestia* Vialov, 1965. Miocene (Burdigalian), Ukraine.

Other Included Species. ◊*Bestiopeda sanguinolenta* Vialov, 1965. Miocene (Burdigalian), Ukraine.

Remarks. The ichnogenus *Bestiopeda* Vialov (1965), based on Burdigalian (Miocene) tracks from Ukraine (*B. bestia*), was first proposed as a form genus to include all fossil carnivore paw-prints. It is here restricted to embrace only feloid tracks in which the claws were normally either short and situated above the plane of the phalangeal pads, or retractile and in which the pad impressions, of fairly uniform size, form a semicircular arc in front of the sole and heel impressions. Following this restriction, the ichnogenus *Pumaeichnium* Aramayo and Bianco (1987) becomes a junior synonym of *Bestiopeda*.

Footprints in which pad-marks are asymmetrical in size and position are assigned to our new miacid-like ichnogenus *Tetrastoibopus*. Footprints in which two of the pad marks lie symmetrically alongside the sole or heel marks are attributed to *Pehuencoichnium* Aramayo and Bianco, 1987. Footprints similar to *Bestiopeda* (as here emended), but with claws uniformly extended, are placed into new genera described below.

SUBORDER CANIFORMIA

FAMILY MUSTELIDAE, incertae sedis

Ichnogenus *Phacelopus* Sarjeant and Langston, nov.

Derivation of Name. Greek *pheklos*, bundle, cluster; *pous*, foot; with reference to the clustered appearance of the digits.

Diagnosis. Plantigrade to semiplantigrade footprints, with five clawed digits on each foot. Manus somewhat smaller than pes. The digits and claws curve inward toward an axis between digits II and III. Digits of manus with one or two phalangeal pads; digits of pes with two or three phalangeal pads. Impressions of metacarpals and some carpals, and of metatarsals and some tarsals, may be distinguishable. Total in-terdigital span of manus (up to 70°) less than that of pes (up to 80°).

Type Species. *Phacelopus therates* Sarjeant and Langston, herein. Late Eocene (Chadronian), Texas.

Remarks. Much confusion exists about the classification of musteloids (including "procyonids") and their distribution in space and time (Schmidt-Kittler, 1981; Martin, 1989). Though skeletal evidence for the group is lacking in west Texas, several genera often re garded as musteloids (e.g., *Plesictus, Palaeogale*) are present in equivalent late Eocene rocks in Colorado, Wyoming and South Dakota. Consequently, in spite of some apparently negative evidence, the similarity of the *Phacelopus* tracks to those of existing mustelids justifies their provisional placement into this group. There is, however, a little canid (*Hesperocyon*) with a foot structure that might have produced tracks like *Phacelopus*. *Hesperocyon wilsoni* is present in slightly higher Chadronian strata (Airstrip local fauna) in the same general area in the Vieja country, so it is not impossible that an ancestor of *H. wilsoni* is responsible for the *Phacelopus* tracks.

Only one report of fossil mustelid tracks is known to us. *Mustelidichnium* Aramayo and Bianco (1987), from the Late Pleistocene of Buenos Aires Province, Argentina, differs from *Phacelopus* in having very short, straight digits and subquadrangular palmar and plantar impressions.

Phacelopus therates Sarjeant and Langston, ichnosp. nov

Plate 8a. Figures 25, 26.

Derivation of Name. Greek *therates*, hunter; in reference to the presumed nature of the trackmaker.

Diagnosis. Plantigrade to semiplantigrade footprints with five moderately long, sharply clawed digits on each foot. Manus somewhat smaller than pes. The digits and claws all curve inward toward an axis between digits II and III. Manual digits I, III and IV bear single, elongate-oval phalangeal pads; digit II appears to bear two pads. Pedal digits I, IV and V bear smaller, elongate pads; digits II and III each bear three pads. Impressions of the metacarpals and some carpals and of the metatarsals and some tarsals may be discerned. Total

interdigital span of manus (under 70°) less than that of pes (over 70°). Trackway moderate; stride long.

Type Specimen. TMM 41500-32, track at position 14, section C of "Grand Junction" slab (41500-22).

Horizon and Locality. See Introduction.

Description. This trackway, of an efficient pedestrian progressing at a steady amble, traverses section C of the slab and fades out on what was apparently the drier ash of Section A. Five footprints are relatively clear, the best being illustrated in pl. 8.

Dimensions. Breadth of trackway 160 mm; pace 280 mm; stride 520 mm. Manus: overall length 100 mm, greatest breadth 82 mm. Length of digits (allowing for curvature): I, 36 mm; II, 49 mm; III, 46 mm; IV, 48 mm; V, 32 mm. Pes: overall length 120 mm, greatest breadth 96 mm. Length of digits: I, 42 mm; II, 68 mm; III, 71 mm; IV, 60 mm; V, 48 mm.

Divarication of Digits. Because of the curvature, measurements are somewhat arbitrary. See fig. 26 for explanation.

Remarks. For discussion of possible affinities, see p. 27.

FAMILY CANIDAE

◊Ichnogenus *Chelipus* Sarjeant and Langston, nov.

Derivation of Name. Greek *chele*, claw; *pous*, foot; with reference to the permanently extended claws.

Diagnosis. Plantigrade to semiplantigrade footprints exhibiting four digits (II to V), each with a spheroidal to ovoidal or elongate digital pad and each giving rise to a prominent claw (permanently extended). The digits form a semicircle in front of, or about the front portion of, sole or heel pads. Digital pads are of equal or similar size. Trackway narrow; stride long.

Type Species. ◊*Chelipus gracilis* (Vialov, 1965) Sarjeant and Langston, n. comb. [= *Bestiopeda gracilis* Vialov, 1965:113; reillustrated and more fully described by Vialov, 1966:134-135, pl. 35 fig. 2]. Miocene (Burdigalian), Ukraine.

Remarks. Following our restriction of Vialov's genus *Bestiopeda* to footprints of feloids with claws normally retracted or held above the plane of footprint impressment (p. 27),

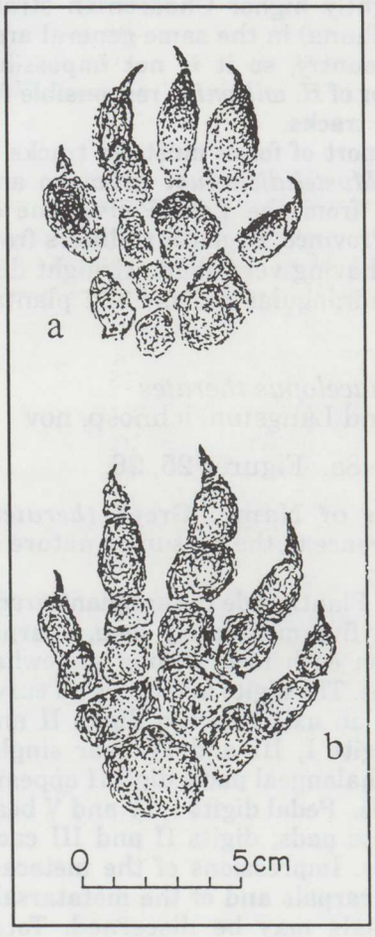


Figure 25. (Left) *Phacelopus therates* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-32. (a) Right manus. (b) Right pes.

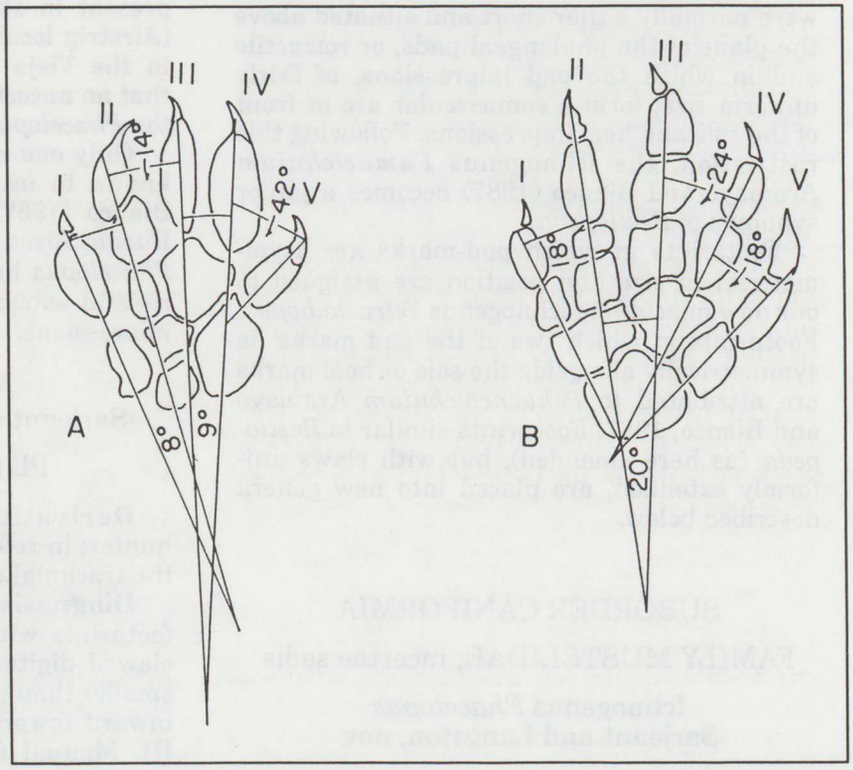


Figure 26.(Above) *Phacelopus therates* Sarjeant and Langston, TMM 41500-32. Interdigital angles. (A) Right manus. (B) Right pes.

a new ichnogenus is here defined to contain similar forms in which the claws are permanently extended—the footprints of canoids (dogs, foxes, wolves and their living or extinct relatives). Since two canids, *Hesperocyon* and *Mesocyon*, are present in the late Eocene of North America, *Chelipus* may be expected in older Paleogene deposits, though it has not so far been reported.

Family AMPHICYONIDAE

Ichnogenus *Axiciapes* Sarjeant and Langston, nov.

Derivation of Name. Latin *axicia*, shears; *pes*, foot; with reference to the resemblance of the hind foot of the type species to partially open shears.

Diagnosis. ?Digitigrade or semiplantigrade to plantigrade footprints, with five digits represented in the forefoot and four (II to V) in the hind foot. Digits of manus widely spread; claws incompletely impressed and probably fully or partly retractile. Digits of pes with claws fully extended; II and III pointing forward, IV and V outward.

Type Species. *Axiciapes ferox* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. Appraisal of these tracks as semiplantigrade to plantigrade is open to question. They may have been digitigrade if the feet were provided with well developed digital and plantar pads (R. Hunt, personal communication, 1990).

The sharp claws of the hind foot clearly mark the trackmaker as a predator. On the forefoot, only the tips of claws are seen, suggesting that they were semi-retractile or that the foot possessed thick digital pads. The concept of partly retractile claws fits well with Scott's interpretation (1913:525-527) of the feet of the primitive canoid *Daphoenus*, the presumed ancestor of the so-called bear-dogs of the later Oligocene and Miocene. The spreading manus Scott depicted (idem., fig. 258) also accords well with the character of these footprints.

The imprint of the pes is puzzling in that it shows no trace of a first digit. However, since the weight of the pes was evidently stressed unequally on its outer side, it may be that digit I was present in the foot, but was held clear of the ground surface during walking. This is further reason to suppose that the foot was more digitigrade than plantigrade. *Daphoenus* was "digitigrade without doubt" (R. Hunt, personal communication, 1990).

Daphoenine amphicyonids, *Daphoenus* cf. *D. lambei* and *Daphoenocyon dodgei*, respectively from the Porvenir l.f. and Little Egypt l.f., as well as an unassigned taxon also from the Porvenir l.f., were reported by Gustafson (1986). Besides the other resemblances noted, the *Axiciapes* tracks are about the right size for some *Daphoenus* species (Hunt, pers. comm., 1990). *Daphoenocyon dodgei* is not well known but was apparently not unlike *Daphoenus* generally. It was a little larger than *D.* cf. *D. lambei*, but the feet of this genus are not reported in the literature. From what positive evidence there is, *Axiciapus* seems more likely to be the track of *Daphoenus* than of *Daphoenocyon*.

Axiciapes ferox Sarjeant and Langston, ichnosp. nov.

Plates 10b-c, 17. Figures 27, 28.

Derivation of Name. Latin *ferox*, fierce; in reference to the predatory nature of the trackmaker.

Diagnosis. ?Digitigrade or semiplantigrade to plantigrade footprints, the manus having five digits, the pes only four (II to V). Digits of manus widely spreading, the interdigital span approaching 50°. III and IV are the strongest digits, I and II more slender, V very slender and distinctly separate. Manus broader than pes, digit II being separated sharply from the others (interdigital angle around 35°); total interdigital span approximately 50°. Claws of manus retracted or held above the ground, only the tips being impressed: claws of pes extended and large, that of II divided and curving inward, those of III and V curving outward, whereas that of digit IV curves inward toward III. Trackway moderate; stride long.

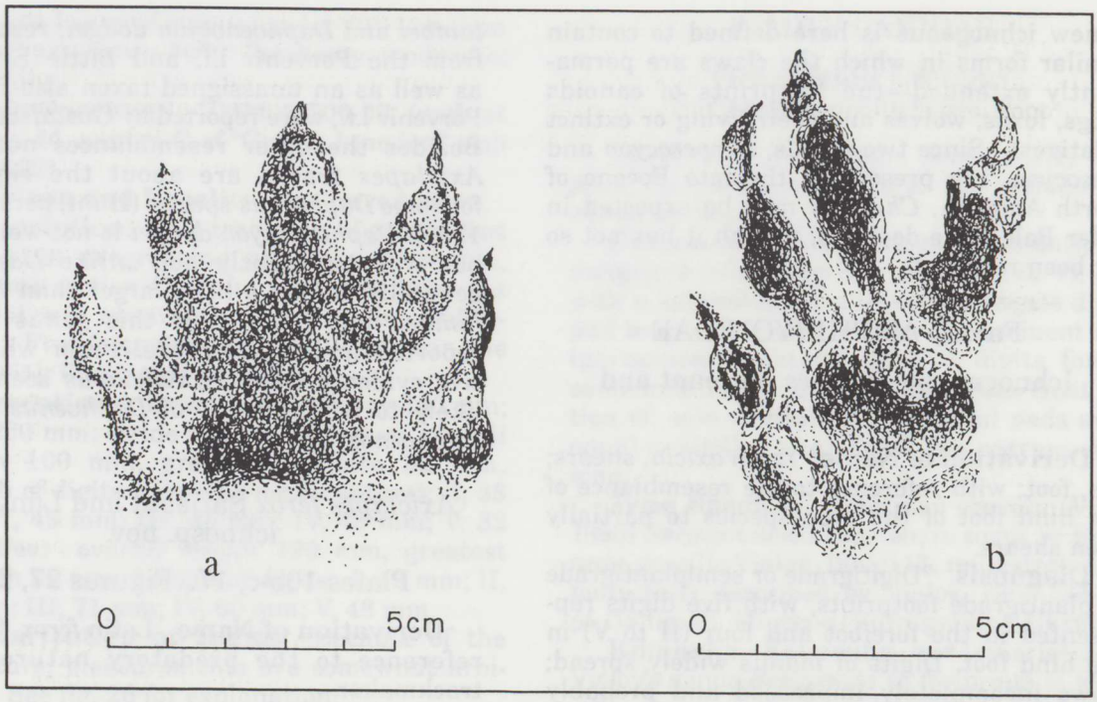
Type specimen. TMM 41500-13.

Horizon and Locality. See Introduction.

Description. The pattern of tracks shows a regular superposition of hind foot imprints on those of the forefoot (see pl. 14). This accords well with the "crab-wise gait" of a dog, as illustrated by Leutscher (1960, fig. 10D).

Dimensions. Breadth of trackway, 123 mm; pace 320 mm; stride 640 mm. Manus: overall length at least 60 mm (since all manus impressions are superposed by pes impressions, the whole manus imprint may be longer); maximum breadth 72.5 mm. Length of digits: I, 20 mm; II, 25 mm; III, 30 mm; IV (curved), 27 mm; V, 40 mm. Pes: overall length 80 mm; maximum breadth 65 mm. Length of digits: II, 34 mm; III, 38 mm; IV (curved), 38 mm; V, 25 mm.

Divarication of Digits. See fig. 28 for de-


a
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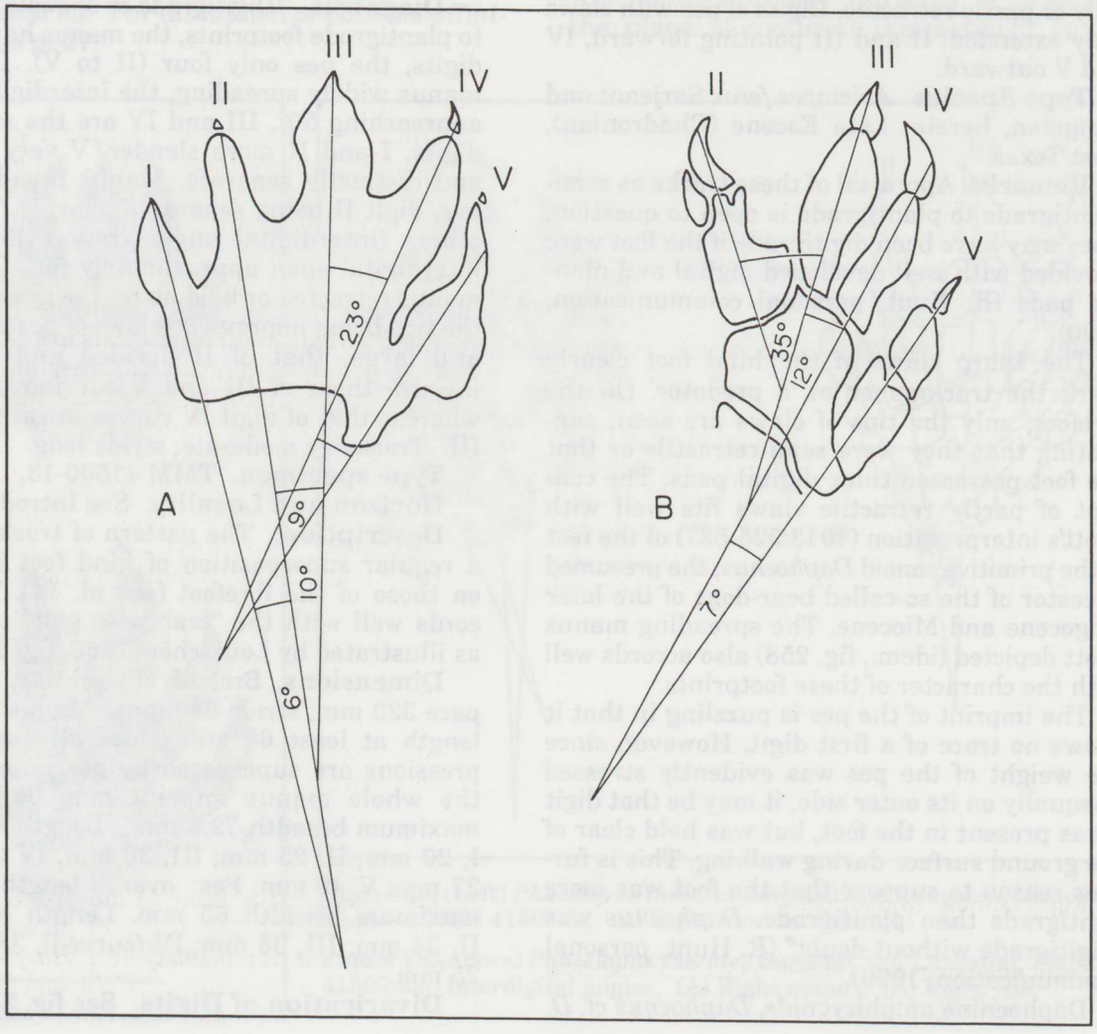
I
II
III
IV
V
23°
9°
10°
6°
A
II
III
IV
V
35°
12°
7°
B

tails. The manual interdigital angle between III and IV is very subjective, since IV curves.

Remarks. The trackmaker may have had the proportions of a long-coupled, medium-sized dog and was evidently moving at a slow trot. For discussion of possible relationships, see under genus (p. 29).

Axiciapes curvidigitatus
Sarjeant and Langston, ichnosp. nov.

Plate 11. Figures 29, 30.

Derivation of Name. Latin *curvatus*, bent; *digitatus*, having fingers; with reference to the curving digits of the forefoot.

Diagnosis. ?Digitigrade or semiplantigrade to plantigrade footprints, the manus having five digits, the pes only four. Digits I to IV of manus show a strong inward curvature, digit V directed outward; claws partly retracted or held above the ground, the tips alone being impressed. Manus impression rounded; pes longer than manus and shovel-shaped. Digits of pes with claws only partly retracted (II to IV) or fully extended (V); digits straighter than those of manus, II to III directed slightly inward, V outward. Trackway moderate; stride presumed moderate to long.

Type Specimen. 41500-33 on "Electric Guitar" slab (41500-15).

Horizon and Locality. See Introduction.

Description. The "electric guitar" slab bears the tracks of three vertebrates. The footprints described here were of an animal traveling in the opposite direction to the other two. They are indicated by lower-case letters on the key to pl. 11. (The low number and the arrangement of the footprints permits measurement of the pace, but not the stride.)

Dimensions. Breadth of trackway 107 mm; pace 242 mm; stride not measurable. Manus: overall length 64 mm, maximum breadth 68 mm. Length of digits: I, 14 mm; II, 22 mm; III, 22 mm; IV, 22 mm; V, 22 mm. Pes: overall length 78 mm, overall breadth 55 mm. Length of digits: II, 21 mm; III, 23 mm; IV, 29 mm; V, 30 mm.

Divarication of Digits. See fig. 30 for explanation. Manual digits too strongly curved for satisfactory measurement.

Remarks. The impressions of the manual claw tips may have been preserved only because the surface was very wet. If other tracks are found elsewhere that formed on drier surfaces, there may be no indication of claws. The question whether such footprints are digitigrade, rather than semiplantigrade to plantigrade, is discussed earlier (p. 29).

Though sufficiently like *Axiciapes ferox* to merit placement into the same ichnogenus, these footprints are dissimilar in relative size and proportions of manus and pes and in details of digital pads, claws and retractility of the claws; consequently they must represent a different species. The possible affinities of these footprints are discussed earlier (p. 29). When recognition of the trackmaker has not been achieved even at generic level, speculation at specific level would be extremely premature.

ORDER MESONYCHIA

Ichnogenus *Corymbipes*
Sarjeant and Langston, nov.

Derivation of Name. Latin *corymbus*, bunch of flowers or fruit; *pes*, foot; with reference to the clustering of the digits.

Diagnosis. Footprints showing a digitigrade to semidigitigrade forefoot and a plantigrade hind foot; all digits have hooves. Four digits (II to V) of the manus are impressed; manual hooves moderately large, digits II to III directed inward, IV forward and V outward. Five pedal digits, together with the whole heel, are impressed; tarsals and metatarsals are sometimes distinguishable in good impressions. Pedal hooves smaller than those of the manus; I is smallest and directed inward, II to IV are directed forward and V outward.

Type Species. *Corymbipes superstes* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. These remarkable hoofed tracks, with four digits on one foot and five on the other, have no parallels among existing ungulate groups having osteological representation in the late Eocene or Oligocene. The disposition of the hooves in these digitigrade to semiplantigrade and plantigrade tracks suggests some archaic ungulate. They are, however, completely unlike what might be expected of *Phenacodus* tracks and hence may be those of a mesonychid.

The Candelaria local fauna from the Colmena Tuff in the Vieja region of west Texas contains a massive mesonychid, *Harpagolestes* cf. *H. uintensis*. According to Wilson (1978), the Candelaria local fauna is of Uinta C age sensu

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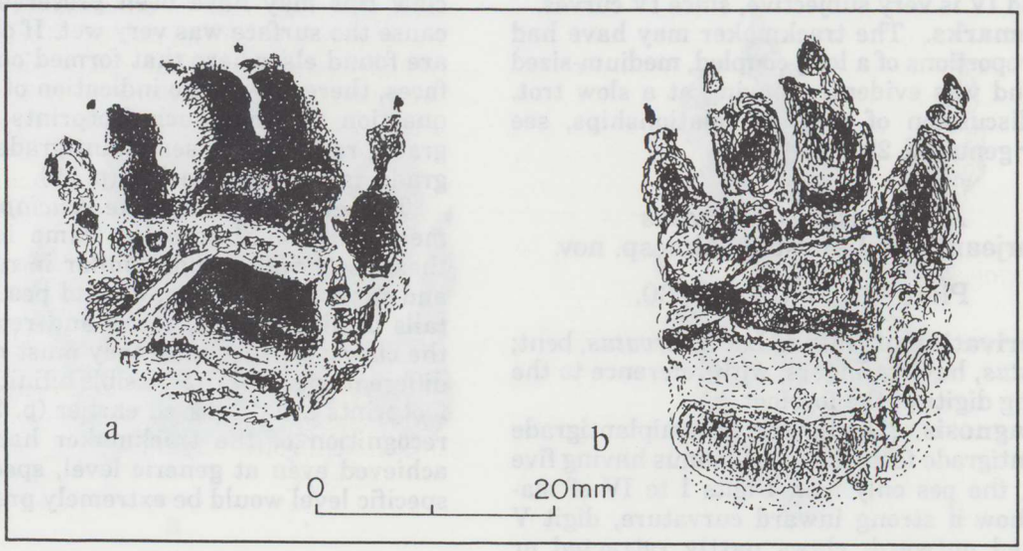
Figure 27. (Facing page, top) *Axiciapes ferox* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-13. (a) Right manus. (b) Left pes.

Figure 28. (Facing page, bottom) *Axiciapes ferox* Sarjeant and Langston, TMM 41500-13. Interdigital angles. (A) Right manus. (B) Right pes (based on left pes, reversed to facilitate comparison).



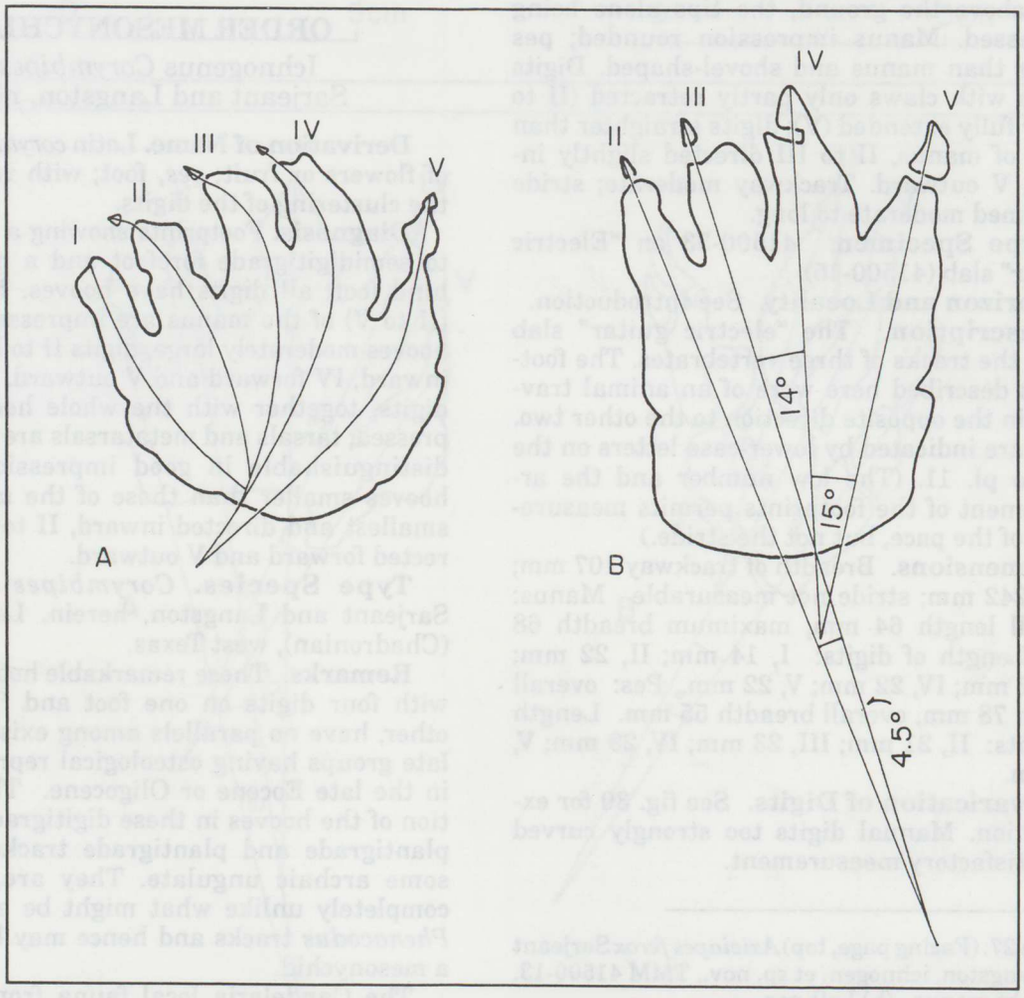


Figure 29. (Top) *Axiciapes curvidigitatus* Sarjeant and Langston, ichnosp. nov., TMM 41500-33. (a) Right manus. (b) Right pes (with crack in rock surface restored).

Figure 30. (Bottom) *Axiciapes curvidigitatus* Sarjeant and Langston, TMM 41500-33. Interdigital angles. (A) Right manus. (B) Right pes.

Emry (1981). The last North American occurrence of *Harpagolestes* is in the middle member of the Devil's Graveyard Formation (the Skyline Channels) of early Duchesnean age. Neither of these late Eocene records is much older than the Porvenir local fauna; moreover, the localities are distant from it only by roughly 50 miles (Wilson, 1986). Consequently, it seems possible that the *Corymbipes* tracks were made by a late surviving mesonychid, if not by *Harpagolestes* itself.

Although the feet of such smaller mesonychids as *Synoplotherium* and *Mesonyx* are well known, those of the larger *Harpagolestes* and *Hessolestes* are virtually unrepresented so far. The only information is Peterson's (1931) comment that the distal end of the second metatarsal of *Harpagolestes uintensis* is more like an ungulate than a carnivore. The feet of *Synoplotherium* and *Mesonyx* were smaller than the trackmaker and *Mesonyx obtusidens* was especially gracile; indeed, Wortman (1901) compares the pes to that of a greyhound. While these smaller forms were probably cursorial, *Harpa-golestes*, because of its large size, was not an "apt" runner (Szalay and Gould, 1966). This statement is surely applicable to the maker of the *Corymbipes* tracks.

Corymbipes superstes
Sarjeant and Langston, ichnosp. nov.

Plates 18, 19a. Figures 31, 32.

Derivation of Name. Latin *superstes*, survivor; with reference to the late persistence of this multi-hoofed ungulate.

Diagnosis. Footprints of moderate to large size, with digitigrade forefeet and plantigrade

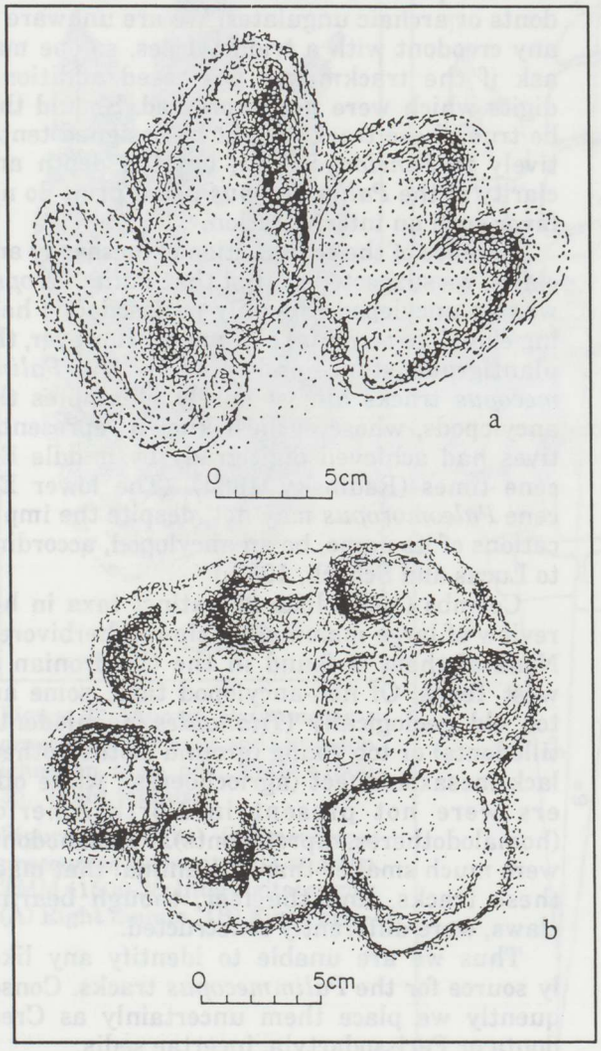


Figure 31. *Corymbipes superstes* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-34. (a) Left manus. (b) Left

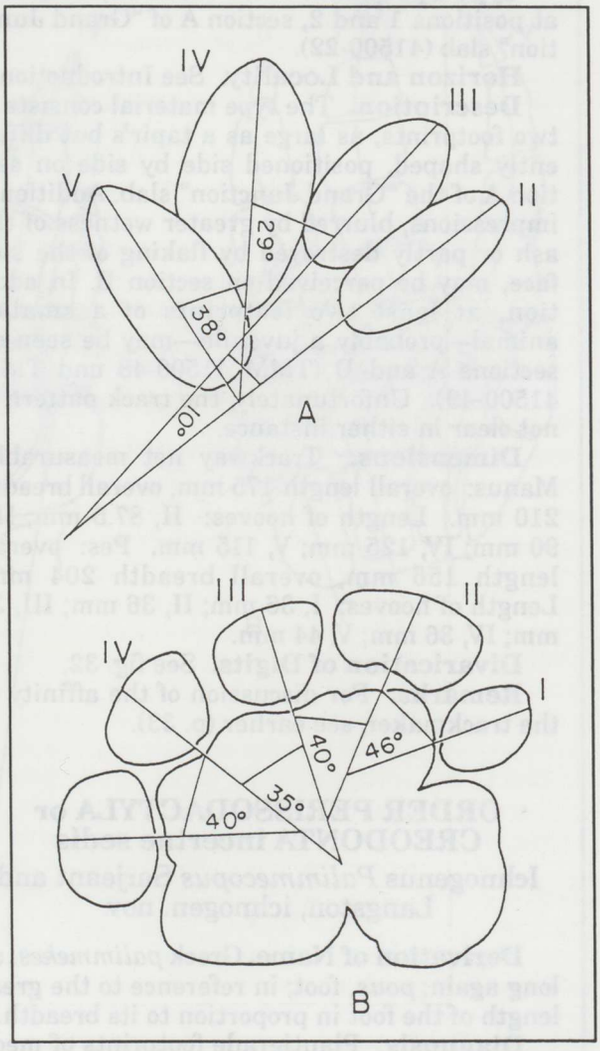


Figure 32. *Corymbipes superstes* Sarjeant and Langston, TMM 41500-34. Interdigital angles. (A) Left manus. (B) Left pes.

hind feet. Four digits (I to IV) of the manus are impressed; all bear ovate hooves. Hooves II and III are of almost equal size, III slimmer than II, both hooves directed obliquely inward; IV, the largest hoof, is directed forward while V, only slightly smaller than IV, is directed outward. Five digits of the pes, together with the whole heel, are impressed; tarsals and metatarsals may be distinguished, the weight borne equally by the whole pes and not predominantly by the hooves. All hooves are relatively small; I is smallest and subcircular, II is transversely elongated, like an outwardly-bent elongate oval; II and III are of almost equal size and ovate; and V is large and rounded to subangular. The hooves of the manus have an interdigital span of around 90° and are considerably larger than those of the pes; the latter are arranged in a semicircle (180°).

Type Specimen. TMM 41500-34, footprints at positions 1 and 2, section A of "Grand Junction" slab (41500-22).

Horizon and Locality. See Introduction.

Description. The type material consists of two footprints, as large as a tapir's but differently shaped, positioned side by side on section A of the "Grand Junction" slab. Additional impressions, blurred by greater wetness of the ash or partly destroyed by flaking of the surface, may be perceived on section B. In addition, at least two footprints of a smaller animal—probably a juvenile—may be seen on sections A and D (TMM 41500-48 and TMM 41500-49). Unfortunately, the track pattern is not clear in either instance.

Dimensions. Trackway not measurable. Manus: overall length 175 mm, overall breadth 210 mm. Length of hooves: II, 87.5 mm; III, 90 mm; IV, 125 mm; V, 115 mm. Pes: overall length 156 mm, overall breadth 204 mm. Length of hooves: I, 36 mm; II, 36 mm; III, 36 mm; IV, 36 mm; V, 44 mm.

Divarication of Digits. See fig. 32.

Remarks. For discussion of the affinity of the trackmaker, see earlier (p. 33).

ORDER PERISSODACTYLA or CREODONTA incertae sedis

Ichnogenus *Palimmecopus* Sarjeant and Langston, ichnogen. nov.

Derivation of Name. Greek *palimmekes*, as long again; *pous*, foot; in reference to the great length of the foot in proportion to its breadth.

Diagnosis. Plantigrade footprints of medium to large size, with long digits terminating in claws. Manus longer and larger than pes, but having a similar, shovel-like shape; the entire palm and sole are impressed. The manus has four digits (II to V). Digits II to IV are long and parallel for much of their length; the foot axis passes through digit III, which is longest. Digit V is greatly reduced, parallel to the prox-imal end of IV and much shorter. The pes has three digits (II to IV), more widely spread than the manual digits. The pedal axis passes through digit III, which is longer and thicker than the others.

Type Species. *Palimmecopus praecursor* Sarjeant and Langston, herein. Late Eocene (Chadronian), Texas.

Remarks. These are among the most perplexing ichnites in the assemblage. Their large size, long-clawed digits, and mesaxony appear to limit possible trackmakers to either creodonts or archaic ungulates. We are unaware of any creodont with a tridactyl pes, so one may ask if the trackmaker possessed additional digits which were not impressed. Should this be true, these tracks might be assigned tentatively to *Zanclonychopus*, but the depth and clarity of the *Palimmecopus* pedal print do not favor such an interpretation.

Because of the combination of mesaxony and claws, we suspected at first that *Palimmecopus* was an ancylopod, the only perissodactyl having claw-like terminal phalanges. However, the plantigrade stance indicated by the *Palimmecopus* tracks almost surely eliminates the ancylopods, whose earliest known representatives had achieved digitigrady by middle Eocene times (Radinsky, 1964). (The lower Eocene *Paleomoropus* may not, despite the implications of its name, be an ancylopod, according to Lucas and Schoch, 1989.)

Coombs (1983) lists 22 extinct taxa in her review of large mammalian clawed herbivores. None of them is found in the Chadronian of west Texas. Of non-ancylopod taxa, some are too old geologically (*Titanoides*, taeniodonts, tillodonts) or too young (ground sloths); others lack mesaxonic feet (agriochoeres); while others were not present in North America (homalodotheres, diprotodonts). Palaeanodonts were much smaller than the animal that made these tracks, and the feet, though bearing claws, were differently constructed.

Thus we are unable to identify any likely source for the *Palimmecopus* tracks. Consequently we place them uncertainly as Creodonta or Perissodactyla, incertae sedis.

Palimmecopus praecursor
Sarjeant and Langston, ichnosp. nov.

Plate 20. Figures 33, 34.

Derivation of Name. Latin *praecursor*, precursor; with reference to the dwindling fifth manual digit of the trackmaker, foreshadowing later forms in which the digit might well be lost entirely.

Diagnosis. Plantigrade footprints of medium to large size, with long digits terminating in claws. Manus somewhat longer and larger than pes, but having a similar shovel-like overall shape. Both palm and sole are clearly impressed and, in some prints, the detail of carpals and metacarpals or of tarsals and metatarsals may be perceived. Manus with four digits; II to IV long and parallel for much of their length, but divergent at their tips; the manual axis passes through digit III, which is longest and strongest. Digits II and IV are somewhat shorter, their length about 80% of that of digit III; digit V is very short, only half the length of digit IV and closely appressed to its proximal end. The three digits of the pes are all long and curving, II and III curving inward, then forward, and IV outward, then forward. Digit III is the longest and strongest, the pedal axis passing through it; II and IV are slimmer and slightly shorter.

Figure 33. (Above) *Palimmecopus praecursor* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-35. Right manus.

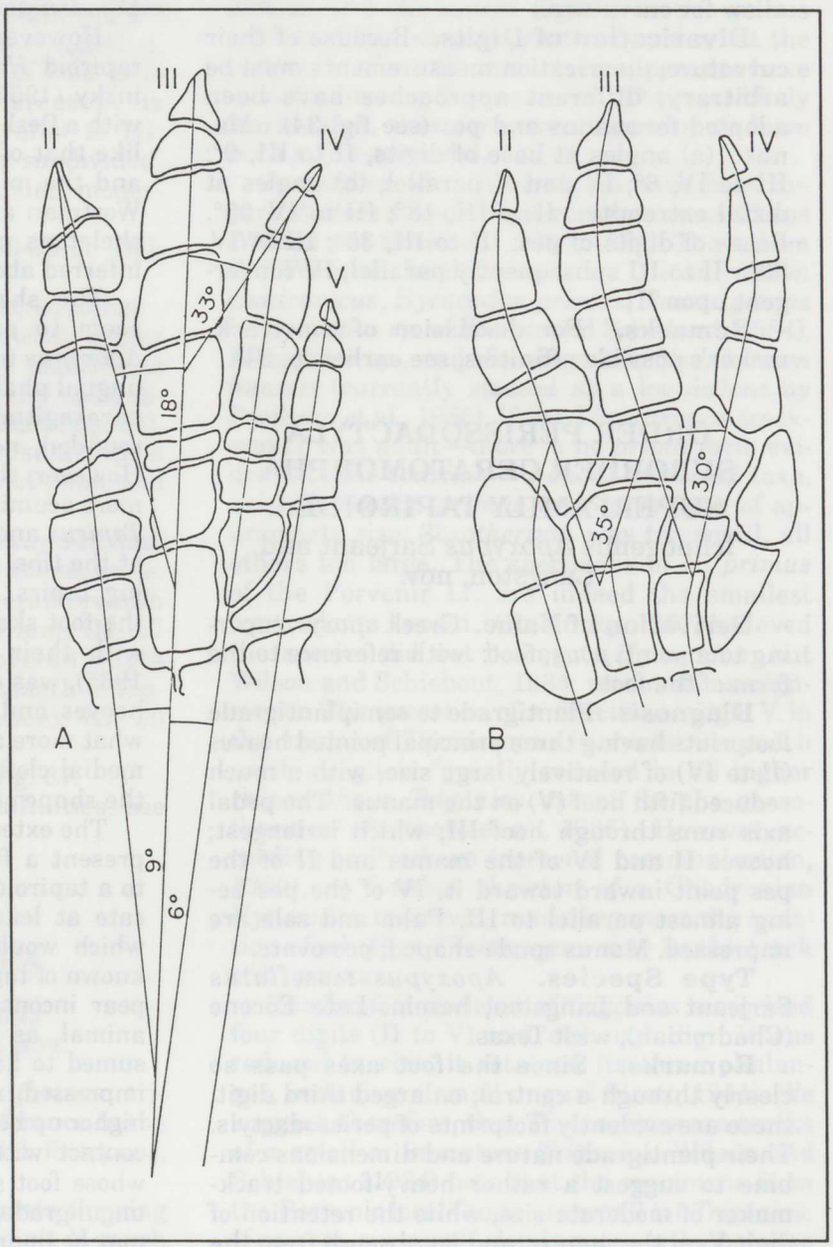


Figure 34. (Right) *Palimmecopus praecursor* Sarjeant and Langston, TMM 41500-35. Interdigital angles. (A) Right manus. (B) Right pes.

Type Specimen. TMM 41500-35, footprints at position 3, section B of "Grand Junction" slab (41500-22).

Horizon and Locality. See Introduction.

Description. The only clear impressions are that of a right manus, with that of a right pes exactly beside it. The rest of the trackway was either off the "Grand Junction" slab, as cast, or not recorded because of drying-out of the surface.

Dimensions. Manus: overall length 286 mm, overall breadth 136 mm. Length of digits: II, 126 mm; III, 150 mm; IV, 122 mm; V, 48 mm. Pes: overall length 258 mm; overall breadth 140 mm. Length of digits: II, 116 mm; III, 136 mm; IV, 122 mm. (Digit measurements allow for curvature.)

Divarication of Digits. Because of their curvature, divarication measurements must be arbitrary; different approaches have been adopted for manus and pes (see fig. 34). Manus: (a) angles at base of digits, II to III, 9°; III to IV, 6°; IV and V parallel; (b) angles at distal extremity: II to III, 18°; III to IV, 35°. Bases of digits of pes: II to III, 35°; III to IV, 30°. II to III subsequently parallel, IV convergent upon III.

Remarks. For discussion of the trackmaker's possible affinities, see earlier (p. 34).

ORDER PERISSODACTYLA
SUBORDER CERATOMORPHA
SUPERFAMILY TAPIROIDEA

Ichnogenus *Apoxypus* Sarjeant and Langston, nov.

Derivation of Name. Greek *apoxys*, tapering to a point; *pous*, foot: with reference to the form of the foot.

Diagnosis. Plantigrade to semiplantigrade footprints having three principal pointed hooves (II to IV) of relatively large size, with a much reduced fifth hoof (V) on the manus. The pedal axis runs through hoof III, which is longest; hooves II and IV of the manus and II of the pes point inward toward it, IV of the pes being almost parallel to III. Palm and sole are impressed. Manus spade-shaped; pes ovate.

Type Species. *Apoxypus tessellatus* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. Since the foot axes pass so clearly through a central, enlarged third digit, these are evidently footprints of perissodactyls. Their plantigrade nature and dimensions combine to suggest a rather heavy-footed trackmaker of moderate size, while the retention of digit V on the manus, and its absence from the pes, strongly suggest the foot of a tapiroid (see Scott, 1913, Figs. 145-146).

Fossil tapir tracks are among the most frequent mammalian ichnites. The presence of the tapiroid *Colodon* in the Porvenir and Little Egypt local fauna might suggest a source for the *Apoxypus* tracks, the size of various *Colodon* species not being inconsistent with this suggestion. However, the feet of *Colodon* are described as remarkably slender and elongate, indicating that "...the genus was on the way to monodactylism, resembling in this respect, *Hyracodon*..." (Scott, 1941:767). Such stilted unguligrade feet are unlikely to have produced the plantigrade to semiplantigrade tracks of *Apoxypus*, so attribution of these tracks to *Colodon* does not seem warranted.

However, the manus of the early Eocene tapiroid *Heptodon*, as reconstructed by Radinsky (1965, fig. 13) might, if provided in life with a fleshy palmar pad, have produced a print like that of *Apoxypus*. Indeed, both *Heptodon* and the mid-to-late Oligocene *Protapirus* (see Wortman and Earle, 1893, fig. 4) had manual skeletons more in keeping with what may be inferred about the structure of *Apoxypus*.

The sharp-tipped hoof impressions may seem to present a problem in attributing *Apoxypus* to the Tapiroidea, since the hoof-like ungual phalanges of existing tapirs leave ovate parasagittal traces whose anterior borders are rounded, not pointed, as in these footprints. However, the ungual phalanges are somewhat more acuminate terminally in *Heptodon* than in *Tapirus* and display a medial parasagittal cleft at the tips, not present in unguals of the existing tapirs. The much lighter construction of the foot skeleton in early tapiroids, coincident with their presumed cursoriality (Radinsky, 1965), was doubtless expressed in less massive hooves and may well have resulted in somewhat more acute anterior tips. (What effect the medial cleft may have had on the unguis and the shape of the hoof is unknown.)

The extensive solar pads on *Apoxypus* prints present a further problem in assigning them to a tapiroid. These structures appear to indicate at least a semiplantigrade foot posture, which would be out of keeping with what is known of tapir foot skeletons. Certainly they appear inconsistent with a lightly-built running animal, as *Heptodon* and *Protapirus* are presumed to have been. Yet the tracks are deeply impressed, so it is conceivable that soft tissue higher up between the digits may have come into contact with the substrate. Even in *Tapirus*, whose foot skeleton may be described as semiunguligrade, the soft tissue between the digits may be impressed in relatively firm substrates.

Apoxypus tessellatus
Sarjeant and Langston, ichnosp. nov.

Plate 21. Figures 35-37.

Derivation of Name. Latin *tessellatus*, inlaid with small square stones, mosaic; in reference to the much-subdivided impressions of palm and sole.

Diagnosis. Plantigrade to semiplantigrade footprints having four hooves on the manus and three on the pes. Manual hooves II to IV are large, the outer hooves convergent upon, and broader than, the central hoof; the fourth hoof (V) is very much smaller and directed outward. All hooves have rather blunt points. The pedal hooves have more acute points; II and III are large and almost lozenge-shaped, IV smaller and having the form of a rounded, asymmetrical triangle. The point of hoof II is directed inward toward III, whereas IV is directed forward and almost parallel to III. Palm and sole impressions much subdivided. Trackway moderate; stride presumed moderate to long.

Type Specimen. TMM 41500-36 on slab 41500-14.

Horizon and Locality. See Introduction.

Description. The type slab shows, rather confusedly, the impressions of the feet of two hoofed animals, both traveling in the same direction (fig. 35, LM_1 and RM_1; pl. 2la-b; fig. 36). The footprints were deeply impressed into a soft surface and show the details of palm and sole with great clarity.

Dimensions. Breadth of trackway 142 mm; pace 328 mm; stride not certainly measurable. Manus: overall length 77 mm; overall breadth 58 mm. Length of digits: II, 22 mm; III, 27 mm; IV, 23 mm; V, 10 mm. Pes: overall length 88 mm; overall breadth 58 mm. Length of digits: II, 24 mm (at median position); III, 30 mm; IV, 18 mm.

Divarication of Digits. See fig. 37.

Remarks. For discussion of affinities, see under genus.

SUPERFAMILY RHINOCEROTOIDEA

Ichnogenus *Thrinaxopus* Sarjeant and Langston, nov.

Derivation of Name. Greek *thrinax*, trident, three-pronged fork: with reference to the three principal digits present in each foot; *pous*, foot.

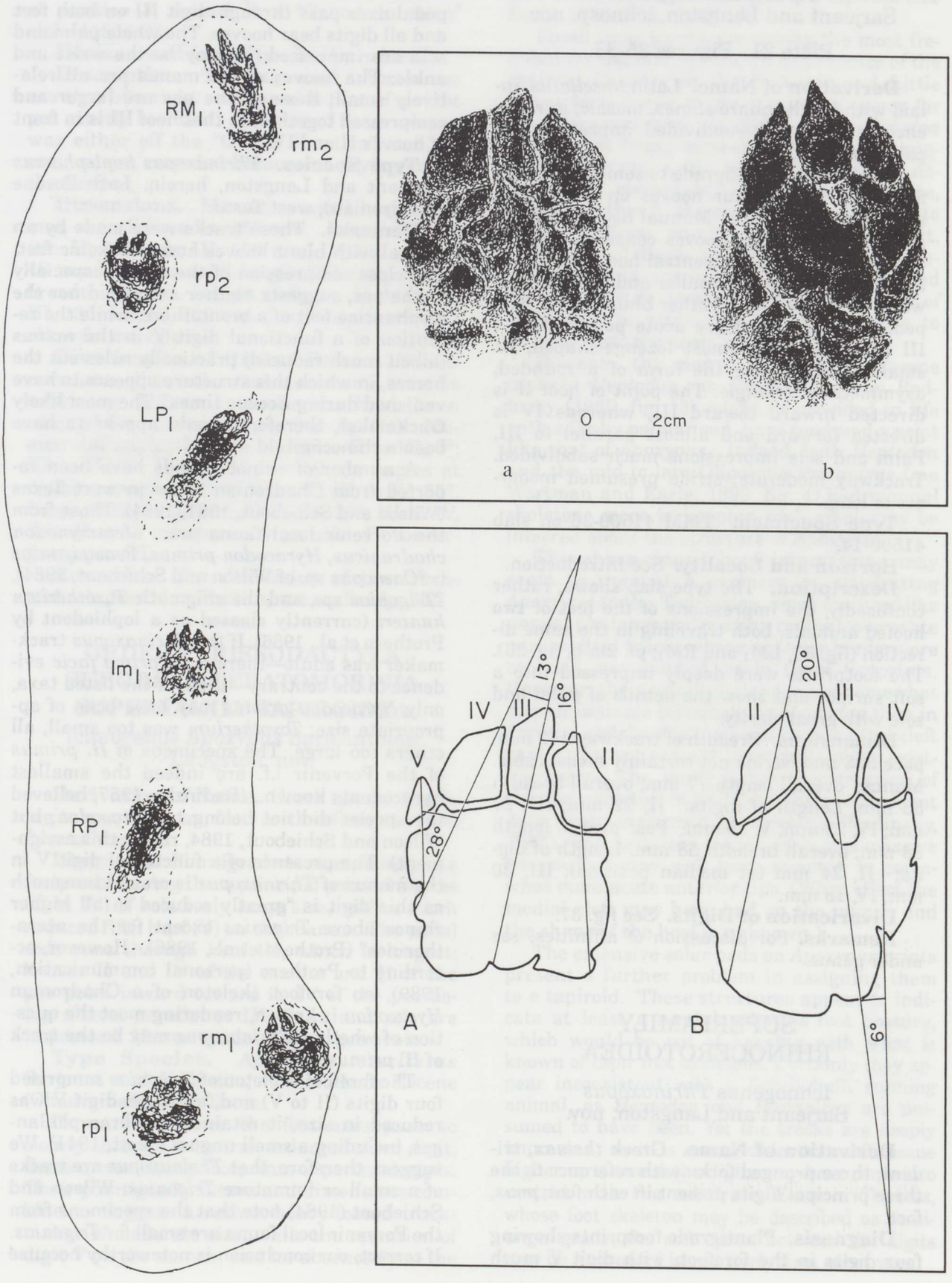
Diagnosis. Plantigrade footprints showing four digits in the forefoot, with digit V much reduced, and three digits in the hind foot. The pedal axes pass through digit III on both feet and all digits bear hooves. The whole palm and sole are impressed, as may be the wrist and ankle. The hooves of the manus are all relatively small; those of the pes are larger and compressed together, so that hoof III is in front of hooves II and IV.

Type Species. *Thrinaxopus hoplephoreus* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. These tracks were made by an animal with blunt hooves and mesaxonic feet. The close compression of the digits, especially in the pes, suggests neither a tapiroid nor the elephantine feet of a brontothere, while the retention of a functional digit V in the manus (albeit much reduced) practically rules out the horses, in which this structure appears to have vanished during Eocene times. The most likely trackmaker, therefore, would appear to have been a rhinocerotoid.

A number of rhinocerotoids have been reported from Chadronian rocks in west Texas (Wilson and Schiebout, 1981, 1984). Those from the Porvenir local fauna are: *Metamynodon chadronicus*, *Hyracodon primus*, *Penetrigonias* (=*?Caenopus* sp. of Wilson and Schiebout, 1984), *?Trigonias* sp., and the enigmatic *Toxotherium hunteri* (currently classed as a lophiodont by Prothero et al., 1986). If the *Thrinaxopus* trackmaker was adult—there is no *prima facie* evidence to the contrary—then, of the listed taxa, only *Hyracodon primus* may have been of appropriate size: *Toxotherium* was too small, all others too large. The specimens of *H. primus* of the Porvenir l.f. are indeed the smallest hyracodonts known. (Radinsky, 1967, believed the species did not belong to *Hyracodon*, but Wilson and Schiebout, 1984, retain this assignment). The presence of a functional digit V in the manus of *Thrinaxopus* is crucial inasmuch as this digit is "greatly reduced in all higher rhinos above *Trigonias* except for the aceratherines" (Prothero et al., 1986). However, according to Prothero (personal communication, 1989), no forefoot skeleton of a Chadronian *Hyracodon* is known, rendering moot the question of whether *Thrinaxopus* may be the track of *H. primus*.

The forefoot skeleton of *Trigonias* comprised four digits (II to V) and, although digit V was reduced in size, it retained its three phalanges, including a small ungual (Scott, 1941). We suggest, therefore, that *Thrinaxopus* are tracks of a small or immature *Trigonias*. Wilson and Schiebout (1984) note that the specimens from the Porvenir local fauna are small for *Trigonias*. If correct, our conclusion is noteworthy because


RM1
rm2
rp2
LP1
lm1
RP1
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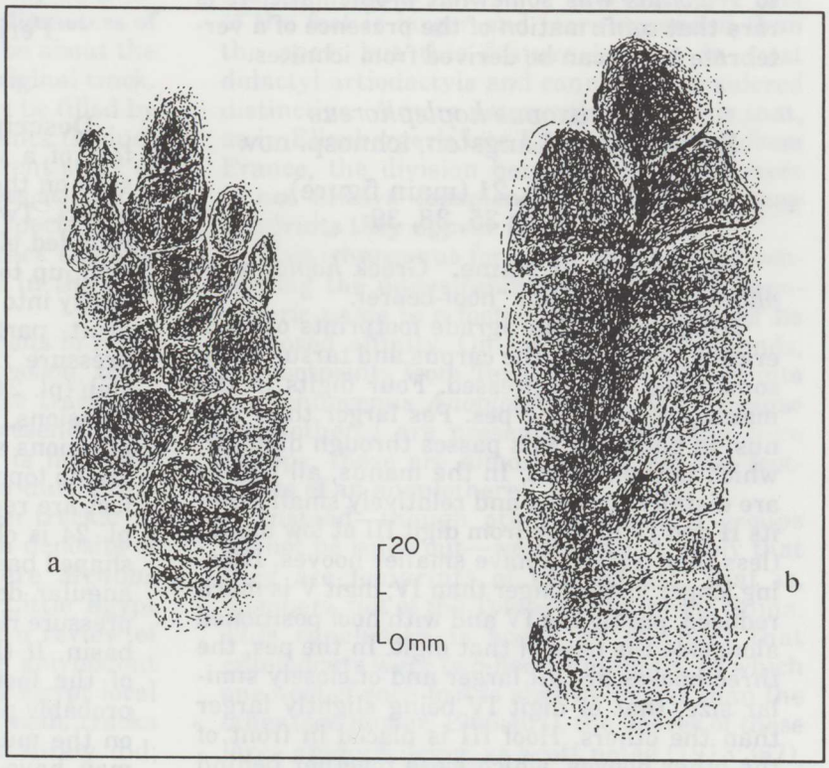

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Figure 35. Interpretative drawing of slab TMM 41500-14, showing the tracks of two hoofed animals traveling in the same direction. Lowercase letters: *Apoxypus tessellatus* Sarjeant and Langston, ichnogen. et sp. nov. (TMM 41500-36). Capital letters: *Thrinaxopus hoplephoreus* Sarjeant and Langston, ichnogen. et sp. nov. (TMM 41500-37).

Figure 36. (Top right) *Apoxypus tessellatus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-36. (a) Left manus. (b) Right pes.

Figure 37. (Bottom right) *Apoxypus tessellatus* Sarjeant and Langston, TMM 41500-36. Interdigital angles. (A) Left manus. (B) Right pes.

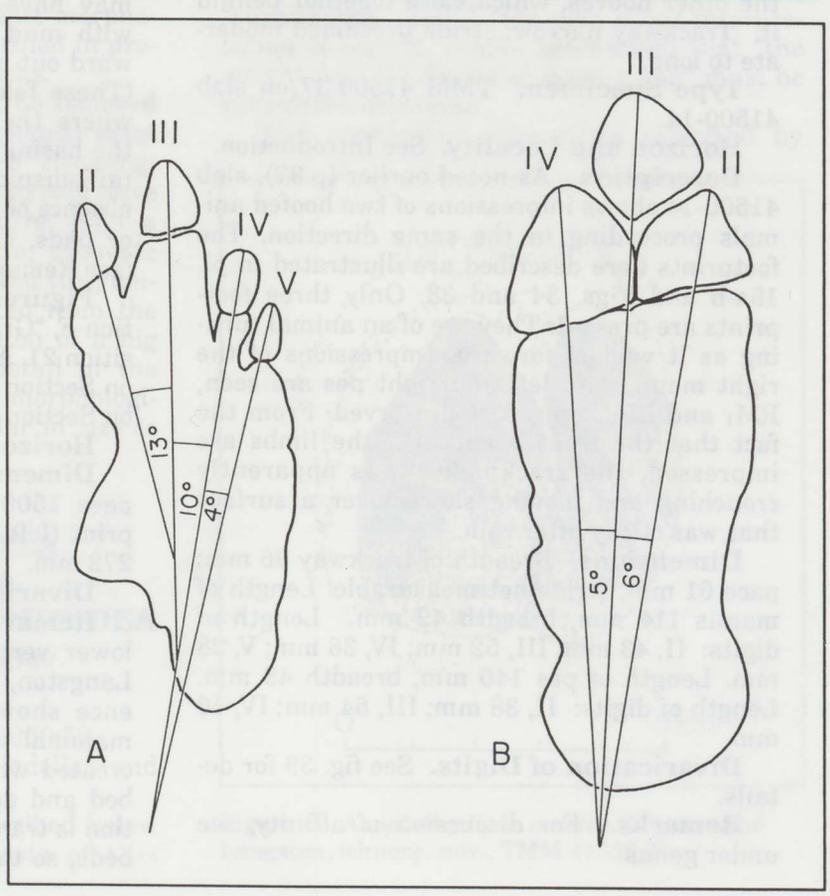


Figure 38. (Above) *Thrinaxopus hoplephoreus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-37. (a) Right manus. (b) Left pes.

Figure 39. (Right) *Thrinaxopus hoplephoreus* Sarjeant and Langston, TMM 41500-37. Interdigital angles. (A) Right manus (B) Left pes.

Wilson and Schiebout's assignment of a jaw and incomplete maxilla with badly worn teeth to *Trigonias* was somewhat problematic. It is rare that confirmation of the presence of a vertebrate taxon can be derived from ichnites.

Thrinaxopus hoplephoreus
Sarjeant and Langston, ichnosp. nov.

Plates 19a-b, 21 (main figure).
Figures 35, 38, 39.

Derivation of Name. Greek *hople*, hoof; *phoreus*, bearer; thus "hoof-bearer."

Diagnosis. Plantigrade footprints of moderate to large size, the carpus and tarsus being sometimes also impressed. Four digits in the manus, three in the pes. Pes larger than manus; in both, the axis passes through digit III, which is the largest. In the manus, all hooves are distally rounded and relatively small. Digits II and IV diverge from digit III at low angles (less than 15°) and have smaller hooves, II being longer and stronger than IV; digit V is much reduced, parallel to IV and with hoof positioned alongside the base of that digit. In the pes, the three hooves are all larger and of closely similar size, that of digit IV being slightly larger than the others. Hoof III is placed in front of the other hooves, which close together behind it. Trackway narrow; stride presumed moderate to long.

Type Specimen. TMM 41500-37 on slab 41500-14.

Horizon and Locality. See Introduction.

Description. As noted earlier (p.37), slab 41500-14 shows impressions of two hoofed animals proceeding in the same direction. The footprints here described are illustrated in pl. 19a-b and Figs. 34 and 38. Only three footprints are present. They are of an animal turning as it walked forward. Impressions of the right manus and left and right pes are seen, RM_1 and LP_1 being best preserved. From the fact that the front portions of the limbs are impressed, the trackmaker was apparently crouching and moving slowly over a surface that was sticky after rain.

Dimensions. Breadth of trackway 96 mm; pace 61 mm; stride not measurable. Length of manus 114 mm, breadth 42 mm. Length of digits: II, 43 mm; III, 52 mm; IV, 36 mm; V, 28 mm. Length of pes 140 mm, breadth 48 mm. Length of digits: II, 38 mm; III, 54 mm; IV, 40 mm.

Divarication of Digits. See fig. 39 for details.

Remarks. For discussion of affinity, see under genus.

cf. BRONTOTHERIIDAE or AMYNODONTIDAE incertae sedis

Perissodactyl Footprint, Type A

Plates 4, 24

Description. Four deep imprints of the feet of a very large, heavy animal are to be seen on the "Grand Junction" slab (at right on pl. 4). Two footprints, separated by a low, rounded elevation, form a single large depression, up to 9 cm deep, where one foot stepped partly into the hollow made by another. A third print, partly bounded on either side by low pressure ridges, occurs near the edge of the slab (pl. 24). In the middle, between these impressions, is a fourth large print. All the impressions are practically featureless and there are no topographic landmarks to indicate what feet are represented. The impression shown in pl. 24 is oblong, comprising a fairly regularly shaped basin at one end and a shallower, rectangular depression (bounded laterally by the pressure ridges) sloping gently into the rounded basin. If the basin represents the impression of the foot at rest, the sloping surface was probably produced by the foot slipping forward on the mud. Alternatively the sloping surface may have been caused by the foot, possibly with mud adhering to it, being dragged forward out of the deeper part of the depression. (These features are not well shown in pl. 4, where the low angle of lighting accentuates the basinal part of the tracks.) The lack of details displayed by the tracks, in particular the absence of any clear indication of digits, hooves, or pads, suggests that they are ghost prints (see Remarks, below).

Figured Specimen. TMM 41500-45, section F, "Grand Junction" slab (41500-22) at position 21. Another footprint can be seen at right on Section F. The double print lies at lower left on Section E: see pl. 4.

Horizon and Locality. See Introduction.

Dimensions. Trackway breadth 1150 mm; pace 1500 mm; stride 2400 mm. Individual print (left manus?): length 448 mm, breadth 272 mm.

Divarication of Digits. Not determinable.

Remarks. Ghost prints have been noted in lower vertebrate tracks (Lessertisseur, 1955; Langston, 1983; Leonardi, 1987), but experience shows that they are also common as mammal and bird ichnites. Such prints are created when an animal steps upon a plastic bed and depresses the surface. The deformation is translated downward through subjacent beds, so that a stack of footprints may be im-

pressed into those beds by a foot that never actually touched their surfaces. Some detail is lost in each layer and each track may be shallower than the one above, but the diameters of the higher underlying tracks may be about the same as, or even larger than, the original track. Subsequently, the actual track may be filled by repeated incursions of fine sediments (including algal mats), forming a superjacent stack of depressions, each one shallower, less acute and smaller than that beneath. Both aspects of the phenomenon are revealed at the track site and are indeed apparently discernible in the four large tracks under discussion.

Although there are faint variations in relief on the bottom of the oblong impression, their significance is unclear. Thus, these tracks do little more than to record the presence of a massive mammal in the area; it is not even certain that the tracks were made during the same episode of wetting as the other tracks.

Of mammals in the Chadronian deposits of west Texas, only the brontothere *Menops* (=*Menodus*) *bakeri* (Porvenir and Little Egypt local faunas; see Mader, 1989, for a review of brontothere taxonomy) and the big amynodont *Metamynodon* (Porvenir and Little Egypt local faunas) are large enough to have made tracks of this size. One of them almost surely did; however, owing to the lack of distinct morphological features, we do not feel justified in proposing a formal name for these tracks.

Chaffee (1943) identified what he believed to be a partial *Brontops*(?) right manus print from the White River Oligocene of Wyoming. This track is so large that it could hardly have been made by any other creature than a brontothere, but it shows separate, subovate digital pad prints with small pointed tips, neither of which might be anticipated from the almost elephantine manual skeleton of a big brontothere. While the lack of detail in the Texas specimens prevents any full morphological comparison, they appear similar in size to the footprint reported by Chaffee.

ORDER ARTIODACTYLA
SUBORDER SUINA
SUPERFAMILY ENTELODONTOIDEA

Ichnogenus *Anoplotheriipus*
Ellenberger, 1980

Anoplotheriipus - Ellenberger, 1980:50.
Entelodontipus - Casanovas-Cladellas and Santafé-Llopis, 1982:117.

Remarks. The footprints described below accord exactly with the diagnosis of this ichnogenus, the hooves being subparallel and the medial hoof (III) having a more acute apex than the lateral hoof (IV). Moreover, the heel of the foot is larger and more expanded than the apex; but this feature is seen in most didactyl artiodactyls and cannot be considered distinctive. A more noteworthy feature is that, as in Ellenberger's late Eocene footprints from France, the division between the two hooves is not always conspicuous, so that in many footprints they appear fused.

This ichnogenus forms an object lesson concerning the undesirability of giving an ichnogeneric name to a footprint on the basis of its supposed affinity. On morphological grounds, the footprints from Texas must be placed into the ichnogenus *Anoplotheriipus*; yet, because anoplotheres are presently known only from Europe, these are almost surely not the footprints of an anoplothere!

Instead—though other artiodactyl groups cannot be ruled out—we consider it likely that they are footprints of entelodonts; that is, members, not of the Tylopoda, but of the Suina. This conclusion is based on the fact that entelodonts were two-hoofed animals, in which one hoof of each foot is slightly bigger than the other (see Romer, 1966:407), the hooves of these large animals being, as Scott noted (1913:367), "surprisingly small." However, if our interpretation is correct, Scott's speculation that "the weight was chiefly borne upon a pad" must be considered disproved.

The entelodont footprints reported by

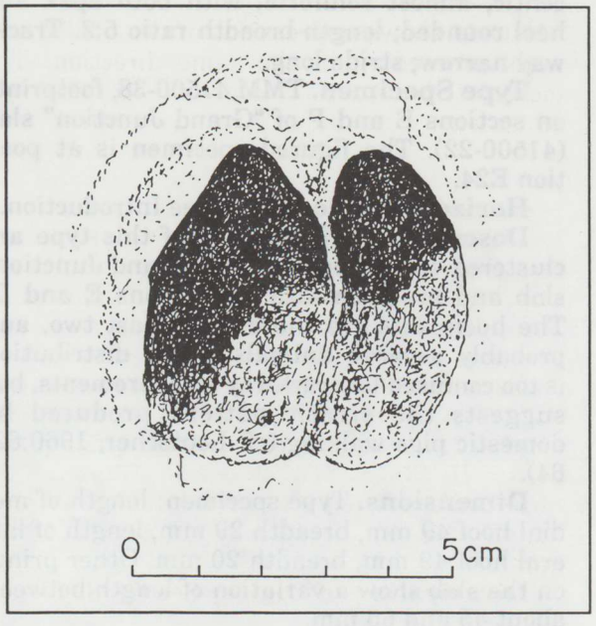


Figure 40. *Anoplotheriipus zeuctus* Sarjeant and Langston, ichnosp. nov., TMM 41500-38.

Casanovas-Cladellas and Santafé-Llopis (1982) from the Oligocene of Spain, and placed by them into the ichnogenus *Entelodontipus* (again named on affinity rather than morphology), show long medial and lateral hooves, which are subparallel and—according to the diagnosis—of equal size. However, their illustrations (ibid., fig. 2 and pl. 2) and measurements show that the two hooves differ slightly in size and shape. *Entelodontipus* differs so little from *Anoplotheriipus* that the ichnogenera are regarded by us as subjective synonyms, with *Anoplotheriipus* the senior taxon.

It should be stressed that the interdigital space widens or contracts according to the relation between the weight of an animal and the hardness of the surface. In consequence, interdigital space should not be used as a prime means for distinguishing ichnospecies, though it may properly be taken into account in diagnoses and descriptions.

Anoplotheriipus zeuctus
Sarjeant and Langston, ichnosp. nov.

Plates 22, 23b. Figure 40.

Derivation of Name. Latinized form of Greek *zeuktos*, yoked; in reference to the close contact between the two hoofprints.

Diagnosis. Double hoofprints in which the medial hoof (III) is larger than the lateral (IV). Medial hoof elongate to subpentagonal in shape, with a subacute apex and flattened-convex heel: length-breadth ratio 5:3. Lateral hoof subcrescentic, almost reniform, with both apex and heel rounded; length-breadth ratio 5:2. Trackway narrow; stride long.

Type Specimen. TMM 41500-38, footprints on sections E and F of "Grand Junction" slab (41500-22). The figured specimen is at position E24.

Horizon and Locality. See Introduction.

Description. Hoofprints of this type are clustered on section F of the "Grand Junction" slab and are seen also on sections E and D. The hoofprints are those of at least two, and probably several, animals. Their distribution is too confused for trackway measurements, but suggests the erratic pattern produced by domestic pigs walking (cf. Leutscher, 1960:62-64).

Dimensions. Type specimen: length of medial hoof 49 mm, breadth 29 mm; length of lateral hoof 49 mm, breadth 20 mm. Other prints on the slab show a variation of length between about 45 and 65 mm.

Divarication of Digits. Because the lateral hoof is so regularly curved, divarication is not measurable.

Remarks. These footprints differ from the supposed anoplothere footprints described by Ellenberger (1980) in the shape of the lateral hoof and its proportional relations to the medial hoof. As noted above, the pattern in the Texas tracks suggests that of a domestic pig walking and differs from the narrower pattern typical of the tracks of cameloids, traguloids or cervoids (see Jaeger, 1948). This is an additional reason for considering these to be entelodont tracks. Their small size suggests that young individuals made the tracks. Since two genera of entelodonts, *Archaeotherium* and *Brachyhyops*, are known from osteological remains in the Chadronian of west Texas (Wilson, 1977), they are the most probable trackmakers. The contemporaneous cameloids, such as *Oromeryx*, were much smaller and retained four digits in the manus, so they can probably be ruled out; however, Webb (personal communication) is uncertain whether *Poebrotherium* would have left "dew claw" traces.

Separate impressions of the hooves are not always seen; identification of the ichnospecies then depends upon the outline of the whole footprint.

Chaffee (1943, pl. 2 fig. 1) illustrated a presumed entelodont footprint from the ?Brule Oligocene of Wyoming. A second footprint, which he thought possibly that of the primitive camelid *Poebrotherium* (ibid., pl. 2 fig. 2), seems to us to be more likely a track of an entelodont. Both footprints resemble the Texas ones in the relative proportions of hooves III and IV, but are dissimilar in the shapes of those hooves; consequently they merit allocation to different ichnospecies.

SUBORDER RUMINANTIA

The classification of fossil didactyl hoofprints presents particular problems to the paleoichnologist, in that mammals attributable to a variety of different artiodactyl groups leave foot-prints that differ only in minor detail, if at all. Heretofore the naming of such footprints has, in almost all instances, reflected an opinion concerning the identity of the trackmaker rather than the actual footprint morphology. This procedure, as noted earlier (pp. 18-19, 41), produces the paradoxical situation that an ichno-generic name reflecting an affinity to one artiodactyl group may need to be applied to footprints of closely similar morphology, but made by a member of a quite different group.

The difficulties are well exemplified by Murie's figure (1954:130) comparing footprints of a variety of different living North American

artiodactyls. Very different animals have footprints that are much alike. In later figures, Murie (ibid., Figs. 133-134) illustrates an additional problem: the fact that the apices of the hooves are parallel or slightly convergent when the trackmaker is walking, but diverge when the animal is galloping or leaping. Morphology thus changes with behavior, not just in the overall track pattern but even in the individual footprint.

We propose herein a revision to the existing classification so that ichnogenera are defined on the objective features of footprint morphology, not upon a subjective judgment concerning their presumed affinity. Unfortunately, the principle of priority requires us to retain the ichnogeneric names that must recognizedly prove quite inappropriate for some of the included species.

Five ichnogenera are revised or described herein and a sixth, *Megalamaichnium* Aramayo and Bianco 1987, accepted without revision. However, since certain known morphologies of didactyl artiodactyl hoofprints have not yet been reported from the fossil record (for example, the kidney-shaped to crescentic hoofprints of many bovoids), the erection of other ichnotaxa will certainly prove necessary in the future.

INFRAORDER PECORA
SUPERFAMILY TRAGULOIDEA or CERVOIDEA

◊Ichnogenus *Pecoripeda* Vialov, 1965, emend. Sarjeant and Langston, nov.

Pecoripeda - Vialov, 1965:114.
Pecoripeda - Vialov, 1966:144.

Emended Diagnosis. Artiodactyl footprints of elongate wedge shape, indicating the presence of two hooves in both manus and pes. Manus and pes of closely similar form, though sometimes of different size. The medial (III) and lateral (IV) hoofprints are always distinct, with axial surfaces sometimes in median or posterior contact, more often separated by a continuous interdigital space. The medial and lateral hooves are exact or mirror images in outline; each is broadest near the heel, tapering to an apex of angular or sharply parabolic outline. Apices of hoofprints directed forward; axes convergent, parallel or divergent according to pace. Maximum breadth of each hoofprint less than 35% of its length.

Type Species. ◊*Pecoripeda gazella* Vialov, 1965. Miocene (Burdigalian), Ukraine.

Other Included Species. ◊*Pecoripeda amalphaea* Vialov, 1965. Miocene (Burdigalian), Ukraine. ◊*Pecoripeda djali* Vialov, 1965. Miocene (Burdigalian), Ukraine.

Remarks. Vialov's overly general diagnosis—"trackways of pair-hoofed horned Pecora, cavicornae, and related groups"—contains no indication of the morphology of the included footprints. It was intended to embrace the tracks of a variety of hoofed didactyl artiodactyls, including traguloids, cervoids and bovoids, and was divided into three subgenera (*Gazellipeda*, *Ovipeda* and *Cervipeda*) on the basis of presumed affinity rather than morphology.

This nomenclature was perhaps acceptable so long as trace-fossils remained "taxonomic outlaws." However, a revision became necessary once they were taken under the aegis of the *International Code of Zoological Nomenclature*. Article 44 specifies that the typical subgenus of any genus should have the same name as that genus; thus the subgeneric name *Gazellipeda*, which includes the type species, should be replaced by *Pecoripeda*. In our view, this invalidates Vialov's whole approach to the subdivision of the genus; in consequence and because of the opinions expressed earlier (pp. 18-19), we reject those subgenera.

The generic diagnosis is here modified to circumscribe the morphology of the type ichnospecies (which Vialov [op. cit.] considered to be footprints of a gazelle-like animal) and that of similar tracks of other fossil and living traguloids and cervoids. The morphology of *P. djali* Vialov 1965, formerly the type species of Vialov's subgenus *Ovipeda*, falls within the emended generic diagnosis. Footprints also of wedge shape, but less markedly elongate and tapering, are transferred to *Gambapes* Sarjeant and Langston, herein. Artiodactyl footprints in which the two hooves diverge sharply toward the anterior, imparting to the whole footprint a rounded-rectangular outline, are placed into *Odocoileinichnium* Aramayo and Bianco, 1987, emend. herein. Artiodactyl footprints with hooves parallel but with hoof apices almost as rounded as the hind portions, the whole footprint having an oval to rounded-rectangular outline, are placed into *Lamaichnium* Aramayo and Bianco, 1987, emend. herein.

◊Ichnogenus *Cervipeda* (Vialov, 1965) emend. Sarjeant and Langston, nov.

Cervipeda - Vialov, 1965:114.
Cervipeda - Vialov, 1966:154.

Emended Diagnosis. Artiodactyl footprints consisting of digital impressions of wedge shape, followed by much smaller, round to rounded-triangular dew claw impressions. Manus and pes of closely similar form, though

sometimes of different size. The medial (III) and lateral (IV) hoofprints are always distinct, though with axial surfaces sometimes in median or posterior contact; more often they are separated by a continuous interdigital space, broadest at the front. The medial and lateral hooves are exact or mirror images in outline; each is broadest near the heel, tapering to an apex of angular or sharply parabolic shape. Apices of hoofprints directed forward; convergent, parallel, or divergent, according to pace. Maximum breadth of each hoofprint more than 35% of its length.

Type Species. ◊*Cervipeda dicroceroides* (Vialov, 1965) Sarjeant and Langston, stat. nov. (=*Pecoripeda* [*Cervipeda*] *dicroceroides* Vialov, 1965:155, pl. 52 Figs. 1a-b). Miocene (Burdigalian), Ukraine.

Remarks. Vialov (op. cit.) distinguished the subgenus *Cervipeda* of his ichnogenus *Pecoripeda* entirely on the presence of dew claw impressions. As a consequence of our revision of the ichnogenus, a reallocation of the type species of the subgenus becomes necessary. In consequence, and since, as Vialov stated, such footprints are typical of the Cervidae, the subgenus is here elevated to ichnogeneric status.

It should be noted from parallels with living deer tracks, however, that while the dew claws are consistently impressed when the deer are leaping or galloping, they may not be impressed when walking, especially on a relatively hard substrate. When the dew claws are not impressed, the footprints may be indistinguishable from those assigned herein to the ichnogenus *Gambapes* Sarjeant and Langston, nov. In such circumstances, it may be impossible to demonstrate their affinity to the Cervoidea; the trackmakers might equally be cameloids or bovoids. The ichnogenus *Cervipeda* is thus defined by behavior as well as by affinity.

SUPERFAMILY CERVOIDEA or BOVOIDEA

◊Ichnogenus *Odocoileinichnium* Aramayo and Bianco, 1987, emend. Sarjeant and Langston, nov.

Odocoelinichnium - Aramayo and Bianco, 1987:537.

Emended Diagnosis. Artiodactyl footprints of rounded-rectangular shape, indicating the presence of two hooves in both manus and pes. Manus and pes of closely similar form, though sometimes of different sizes. The axes of the medial (III) and lateral (IV) hoofprints are sharply divergent, with a V-shaped space between apices directed obliquely to the median axis of the footprint, so that they form its front "corners"; their axial surfaces are in posterior contact. Each hoofprint is broadest near the heel, tapering to an apex of angular or sharply parabolic outline. Maximum breadth of each footprint greater than 35% of its length.

Type Species. ◊*Odocoileinichnium commune* Aramayo and Bianco, 1987. Late Pleistocene, Argentina.

Remarks. Aramayo and Bianco (op. cit.) furnished a combined generico-specific diagnosis that was applicable only to the footprints they were describing (believed to be those of a deer related to the "Virginia deer" *Odocoileus*). The diagnosis is here emended to embrace other footprints of comparable morphology, though not necessarily of like affinity. This ichnogenus differs from *Megalamaichnium* Aramayo and Bianco (1965:536-537) in that the hoofprint apices of *Megalamaichnium* are directed laterally to the axes of the hooves, rather than forward or obliquely.

INFRAORDER TYLOPODA or PECORA

SUPERFAMILY CAMELOIDEA or BOVOIDEA

◊Ichnogenus *Lamaichnium* Aramayo and Bianco, 1987, emend. Sarjeant and Langston, nov.

Lamaichnium - Aramayo and Bianco, 1987: 535-536.

Emended Diagnosis. Artiodactyl footprints of rounded-rectangular shape, indicating the presence of two hooves in both manus and pes. Manus and pes of closely similar form, though sometimes of different size. The medial (III) and lateral (IV) hoofprints have axes that are parallel, with a narrow, linear interdigital space, the apices always directed forward. Axial surfaces of hoofprints flat to slightly concave; abaxial surfaces slightly to markedly convex. Hoofprints widest near the heel, but tapering only to minor degree between the heel and the apex; heel rounded, apex rounded or forming a broad parabolic curve. Maximum breadth of each footprint always greater than 35%, most often greater than 50%, of its length.

Type Species. ◊*Lamaichnium guanicoe* Aramayo and Bianco, 1987. Late Pleistocene, Argentina.

Remarks. Aramayo and Bianco (op. cit.) furnished a combined generico-specific diagnosis that was applicable only to the footprints they were describing (believed to be those of a guanaco [*Lama guanicoe*]). The diagnosis is here emended to embrace other footprints of

comparable morphology, though not necessarily of the same affinity.

SUPERFAMILY UNCERTAIN

Ichnogenus *Gambapes* Sarjeant and Langston, nov.

Derivation of Name. Latin *gamba*, hoof; *pes*, foot.

Diagnosis. Artiodactyl footprints of wedge shape, indicating the presence of two hooves in both manus and pes. Manus and pes of similar form, though sometimes of different size. The medial (III) and lateral (IV) hoofprints are always distinct, with axial surfaces sometimes in median or posterior contact, more often separated by a continuous interdigital space. The medial and lateral hooves are mirror images in outline; each is broadest near the heel, tapering to an apex of angular or sharply parabolic outline. Apices of hoofprints directed forward; axes convergent, parallel or divergent, according to pace. Maximum breadth of each hoofprint greater than 35% of its length.

Type Species. *Gambapes hastatus* Sarjeant and Langston, herein. Upper Eocene (Chadronian), west Texas.

Other Species. ◊*Gambapes satyri* (Vialov, 1965) Sarjeant and Langston, comb. nov. (=*Pecoripeda* [*Ovipeda*] *satyri* Vialov, 1965:114, pl. 16 fig. 2). Miocene (Burdigalian), Ukraine.

Remarks. This ichnogenus differs from *Pecoripeda* Vialov, 1965, emend. herein in having shorter hooves and from *Cervipeda* (Vialov, 1965) emend. herein in lacking accompanying impressions of dew claws. Since it is intended to embrace didactyl footprints made by cameloids, traguloids, cervoids and bovoids, it is here classed as "superfamily uncertain" and given a name that does not indicate any particular affinity.

Gambapes hastatus Sarjeant and Langston, ichnosp. nov.

Plate 6c. Figures 41, 42.

Derivation of Name. Latin *hastatus*, spear-shaped.

Diagnosis. Didactyl artiodactyl footprints of small to medium size, without pads. Manus and pes closely similar in size and form, the lateral hoof (IV) being placed slightly further forward than the medial (III). The apices of the hooves of the manus are typically convergent, giving an overall heart shape to the footprint. The hooves of the pes are subparallel, separated by a larger interdigital space than those of the manus. (However, on soft ground the manus hooves may spread farther apart and become subparallel, like those of the pes.) Front part of axial surface flat, back part curving gently outward; abaxial surface asymmetrically convex, the outermost part of the curve being toward the posterior. Apices rounded-acute; heels rounded. Trackway narrow; stride long.

Type Specimen. TMM 41500-20.

Horizon and Locality. See Introduction.

Description. This slab shows part of a trackway made by an animal while walking quickly or galloping, the print of the pes being placed ahead of the manus and the weight falling on the apices of the hooves (see Murie, 1954, fig. 134 for a modern analog).

Dimensions. Manus: overall length 21.5 mm, greatest breadth 16.5 mm. Medial hoof: length 21 mm, maximum breadth 7.5 mm. Lateral hoof: length 20.5 mm, maximum breadth 7.5 mm. Pes: overall length 21.25 mm, greatest breadth 21 mm. Medial hoof: length 21 mm, maximum breadth 8 mm. Lateral hoof: length 21 mm, maximum breadth 8 mm.

Divarication of Digits. See fig. 42.

Remarks. These small, symmetrical, subequal didactyl hoofprints immediately call to mind primitive camels, in which the fleshy, spreading pads of later camels were not yet developed (Webb, 1972). In such genera as *Eotylopus* and *Poebrotherium*, for example, the unguals were more like the hooves of the contemporary ruminants than those of more advanced camels. Of camelids in the Porvenir local fauna, *Eotylopus* cf. *E. reedi* seems the best candidate as maker of the *Gambapes hastatus* tracks. Known *Eotylopus* forefeet contained four digits of which III and V were only "dew claws," their metacarpals being "greatly reduced and unserviceable" (Scott, 1940:608). The feet of *E. reedi* from the "Titanotherium beds" of Wyoming are about the size indicated by the tracks from west Texas (see Matthew, 1910, Figs. 4, 5); the feet of *Eotylopus* cf. *E. reedi* are unknown.

Other oromerycine camels are poorly represented in the earlier Chadronian local faunas in west Texas. A single upper molar from the Porvenir local fauna, assigned to *Oromeryx* sp., gives evidence of a very small animal, well under the size of the *G. hastatus* trackmaker. Also possible as the trackmaker is another small ?camelid in the Porvenir local fauna, *Hydrosotherium transpecosensis*. Known only from skull and jaws, it has been compared to *Leptomeryx* and *Poebrotherium*; however, its assignment to the Camelidae is tentative (Wilson, 1974).

The well-known camel *Poebrotherium* is present only in the somewhat younger Chadronian Airstrip local fauna and, for this reason, is

judged less likely to have produced the *Gambapes hastatus* tracks. However, tracks of *Poebrotherium* may resemble *Gambapes*, to judge from the feet of *Poebrotherium labiatum* (see Scott, 1941, pl. 65 Figs. 8 and 12).

Other artiodactyls in the Porvenir, Little Egypt and Rancho Gaitan local faunas are traguloids and oreodonts. Traguloids can be ignored as possible trackmakers because of their small size, the characteristic disparity in the size of their front and back limbs, and the likelihood that the forefoot print would show traces of "lateral" toes.

The feet of the small Porvenir, Little Egypt and Rancho Gaitan oreodonts *Bathygenys*, *Limnenetes* and *Aclistomycter* are virtually unknown. It is uncertain whether, any of them had functionally didactyl feet, but an incomplete *Bathygenys* hind foot from the Reeves Bonebed (TMM 40209) has two large and massive "central" metatarsals, whereas the fifth metatarsal is relatively weak. This is a considerable departure from conditions in another small oreodont, *Leptauchenia*. If didactyl, the *Bathygenys* pes might have made a track like *Gambapes hastatus*, but it is very doubtful that an animal with the limb-to-body proportions of oreodonts could have produced such "overstepped" and closely spaced fore-and-aft impressions.

Most of the artiodactyl hoofprint ichnospe-

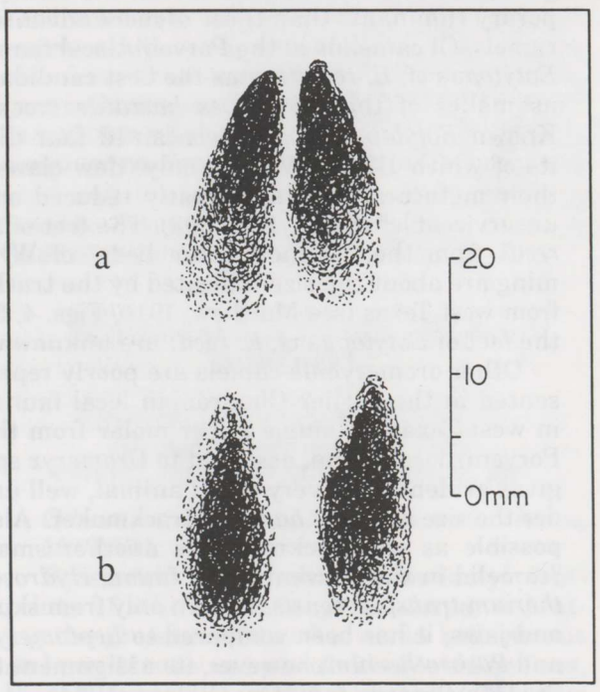


Figure 41. *Gambapes hastatus* Sarjeant and Langston, ichnosp. nov., TMM 41500-20. (a) Manus. (b) Pes.

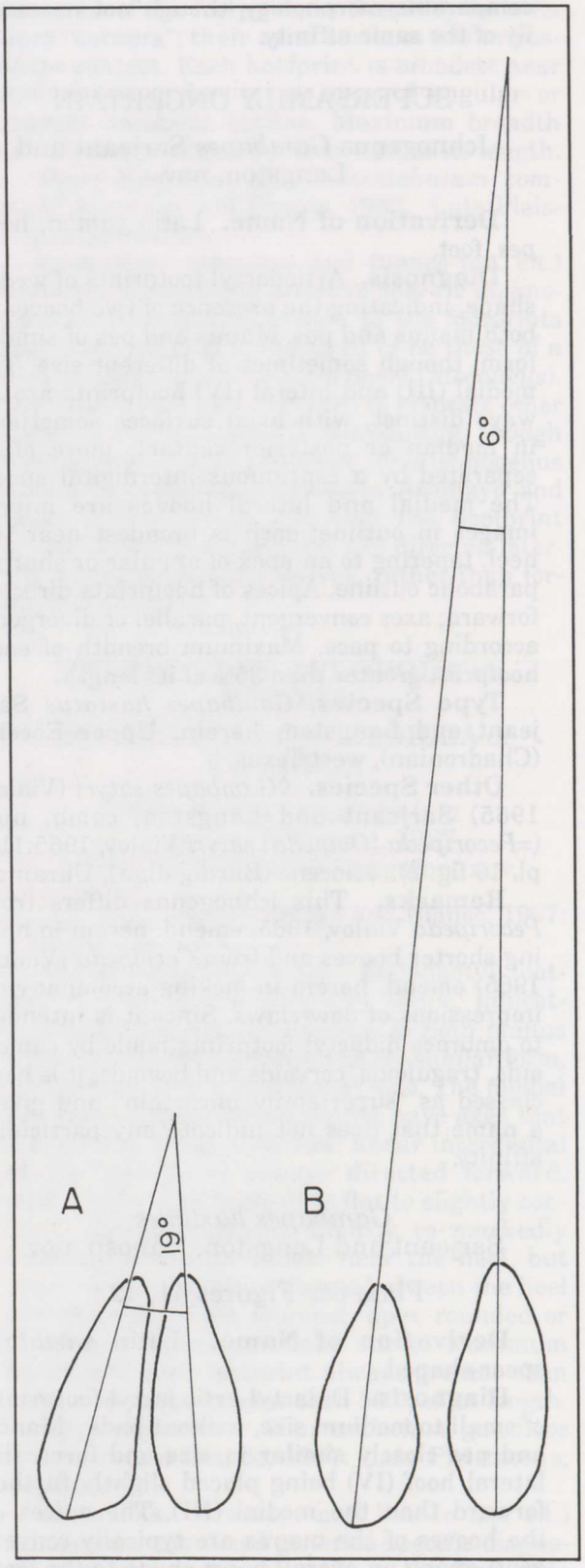


Figure 42. *Gambapes hastatus* Sarjeant and Langston, TMM 41500-20. Interdigital angles. (A) Manus. (B) Pes.

cies described by Vialov (1965, 1966) from the Miocene of Ukraine, the majority are more elongate than those of *Gambapes hastatus*. Most similar are *G. satyri* (Vialov, 1965) Sarjeant and Langston, herein, considered by Vialov to be the footprint of a sheep, and *Cervipeda dicroceroides* (Vialov, 1965) Sarjeant and Langston, herein, regarded by Vialov as that of a deer. *G. satyri* differs in having a concave, not straight, front axial surface on the hooves, while *G. dicroceroides* tracks are proportionately shorter and broader. The tracks illustrated by Robertson and Sternberg (1942), from the presumed Pliocene of Kansas, include one footprint (their fig. 4, lower left) doubtfully considered to be that of a camel. This appears similar to the Texas tracks, but their illustration and description are not adequate for precise comparison.

ORDER RODENTIA

Remarks. The abundance of rodent tracks at the west Texas track site is unique, since fossil rodent footprints are virtually unreported in the literature. The richness of this track fauna is not surprising, however, because rodents are by far the most diverse group identified from skeletal material in the Chadronian deposits in the region. Fifteen genera and nineteen species, representing between five and seven families, have been recognized in the Porvenir and correlative local faunas (Wood, 1974; Wilson, 1978).

However, we are unable to place most of the tracks taxonomically, owing to blurring, lack of possibly diagnostic details, or failure to correspond with any known skeletal remains. It may even be argued that assignment of some of the trackmakers to the Sciurognathi is unwarranted on the evidence. We decided to do so because almost all of the taxa of Early Tertiary rodents identified from body fossils in west Texas belong to the Sciurognathi. The possible exception, *Prolapsus*, the oldest (middle Eocene) hystricognathous rodent known (Wood, 1972; 1973), is under reinvestigation by Wilson and Runkel, who will argue for its reassignment to the Sciurognathi (J. Wilson, personal communication, 1989).

SUBORDER SCIUROGNATHI
FAMILY ISCHYROMYIDAE

Ichnogenus *Ptyariopus* Sarjeant and Langston nov.

Derivation of Name. Greek *ptyarion*, a winnowing fan, dim.; *pous*, foot. In relation to the fan-like spread of the digits of the hind foot.

Diagnosis. Plantigrade footprints of moderate size, in which all five digits are represented. Pes somewhat longer than manus. In the manus, digit I is reduced and opposed; digits II to IV are slender and longer; and digit V is very much reduced. All five digits of the pes are slender, radiating in fan-like fashion with the hallux somewhat opposed; digits I and V are somewhat reduced. All digits bear claws. Trackway narrow; stride moderately long.

Type Species. *Ptyariopus aichmanticheirus* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. These tracks are generally similar to those of large extant rodents (e.g., the coypu *Myocastor*: see Leutscher, 1960.136). They compare well with tracks of the muskrat *Ondatra* (see Murie, 1974, fig. 88) and, except for the absence of webbing on the pes, with the beaver *Castor* (ibid., fig. 87). Resemblances to these taxa include the presence of five digits, with claws too small to be those of carnivores; the great reduction of digits I and V in the manus, though not in the pes; the wide spread of the digits; and the irregular pattern of the footprints, with the hind feet impressions placed beside, on top of, or ahead of those of the forefeet. In size these footprints are closest to the coypu, an animal which may weigh up to 9 kg (Burton, 1962). Two large rodents in the Porvenir local fauna approximate this size: *Leptotomus gigans* and *Pseudotomus johanniculi*, both ischyromyids about the size of the porcupine *Erethizon dorsatum*.

A third form, *Eutypomys inexpectatus*, a rodent of uncertain position but sometimes regarded as a castoroid, deserves mention because of the beaver-like qualities of the *Ptyariopus* tracks. It is the most common rodent in the Porvenir and correlative local faunas. *Ptyariopus* tracks are, however, larger than would be expected from *E. inexpectatus*, which was about the size of a muskrat. Moreover, a number of features noted by Wood (1937) in the pes of *Eutypomys* appear inconsistent with the pedal track of *Ptyariopus*: the first two digits in *Eutypomys* are long and very slender as compared to the other three, and the hallux is "remarkably long and slender" and was not opposable. The axis of symmetry in *Ptyariopus* passes through the third digit and there is no indication of a cat-like flexibility in digits IV and V, as has been inferred for *Eutypomys*. In consequence, the *Ptyariopus* tracks cannot have been made by *Eutypomys*.

The manus of *Leptotomus* is known from the relatively small upper Eocene *L. leptodus*. The specimen described by Wood (1962) has a short

and strongly divergent first metacarpal. Although the rest of the pollex is missing, Wood believed it to have been "fairly strong" and "divergent," and considered that, "together with the generally broad manus and divergent pisiform, [it] suggests a climbing use of the hand" (Wood, 1962:70). Elsewhere, however, he infers (p. 72) from the heavy forelimbs, broad manus and elongate ungual phalanges that *Leptotomus* was fossorial. The massive hind limb and a certain degree of "rotation" of the foot are offered as confirmation of this interpretation.

Judging from the other ischyromyid hands, with their short and sharply divergent pollices, we believe that the long, opposed pollex impression of *Ptyariopus* is unlikely to have been made by such a structure. The same may be said about the somewhat opposed hallux print.

Pseudotomus johanniculi was a robust manitshine (Korth, 1985) which possessed strong feet and moderately compressed claws. It may thus have resembled *Manitsha,* to which genus it was originally assigned (Wood, 1974). Manus and pes skeletons of manitshines are reasonably well known (see Wood, 1962; Simpson, 1941). However, the pollex is unknown in *Manitsha*, but in other ischyromyids where it is known (albeit from the first metacarpal only [*Pseudotomus robustus*, *P. petersoni*]), it has been reconstructed as either very short and divergent (*P. robustus*) or not divergent (*P. petersoni*; see Wood, 1962, Figs. 62 and 67, respectively). The manual skeleton of *Manitsha tanka* figured by Simpson (1941, fig. 3) can indeed, when reversed, be superimposed reasonably well on the manus print of *Ptyariopus*, with allowance for the possible discrepancy in the outline of the pollex. However, the powerful claws characteristic of *M. tanka* were apparently less strongly developed in the maker of the *Ptyariopus* tracks.

The pes skeleton of *Pseudotomus robustus* figured by Wood (1962, fig. 75) seems to conform well to the *Ptyariopus* footprint. Although the foot is not described by Wood, his illustration indicates that the distal end on metatarsal I may have been asymmetrical, the articular ball for the first phalange being developed laterally rather than parasagittaly as in the other metatarsals. Perhaps this means that the hallux was somewhat opposed, as in the *Ptyariopus* tracks; however, the distal end of another met-atarsal, I figured by Wood (fig. 64F), appears to be more symmetrical and any opposability is not evident.

Although clearly speculative, the above analysis leads to the conclusion that the *Ptyariopus* tracks, albeit somewhat larger than would be expected from the *Pseudotomus johanniculi* remains so far discovered, were made by a robust manitshine ischyromyid. *P. johanniculi* seems the most likely candidate among them. Most authors have concluded from the structure of the feet and claws and the massive muscle scars, particularly on the forelimb bones, that members of the tribe Manitshini were slow-moving terrestrial and fossorial or "subfossorial" animals. The tracks of *Ptyariopus* contribute no evidence for or against this idea.

Ptyariopus aichmanticheirus Sarjeant and Langston, ichnosp. nov.

Plate 23a-b. Figures 43, 44.

Derivation of Name. Greek *aichme*, point of a spear; *anticheiros*, thumb: with reference to the pointed shape of the pollex.

Diagnosis. Plantigrade footprints of moderate size, with pes somewhat larger than manus and with more slender digits. The pollex is reduced, greatly thickened and sigmoidally curved inward; manual digits II and III are longer than the pollex and relatively slender; digit V is very much reduced, less than half the length of digit IV. In the pes, all digits are slender; digit III is longest, digits I and V somewhat reduced. All digits show claws, those of the pes larger and somewhat less acute than those of the manus. The front parts, or the whole, of palm and sole are impressed; metacarpals and carpals may be distinguishable. Trackway moderate and rather sprawling; stride long.

Type Specimen. TMM 41500-43, tracks on section C of "Grand Junction" slab (41500-22) at positions 9 and 12.

Horizon and Locality. See Introduction.

Description. These footprints form a trail across the upper part of section C of the "Grand Junction" slab. Some are partially obliterated by cracks or surface flaking and some (e.g., pl. 23a) by sediment that had apparently adhered to palmar and plantar surfaces. The footprints shown in pl. 23b are the best preserved and should be regarded as the types.

Dimensions. Breadth of trackway 315 mm, pace 890 mm, stride 1235 mm. Manus: overall length 79 mm, greatest breadth 71 mm. Length of digits: I, 24 mm; II, 41 mm; III, 35.5 mm; IV, 33 mm; V, 10.5 mm. Pes: overall length 89.5 mm, greatest breadth 75 mm. Length of digits: I, 35.5 mm; II, 54 mm; III, 56.5 mm; IV, 49.5 mm; V, 27.5 mm.

Divarication of Digits. See fig. 44 for details. Manus: pollex curves sigmoidally, the angle varying from 5° between I and II at base

to 37° at the distal extremities. Since the hind foot digits are highly flexible, these angles may vary greatly.

Remarks. For consideration of affinities, see under genus (p.47).

FAMILY UNDETERMINED

Ichnogenus *Tricorynopus* Sarjeant and Langston, nov.

Derivation of Name. Latinized form of Greek *treis*, three; *koryne*, club, mace; *pous*, foot; in reference to the three digits.

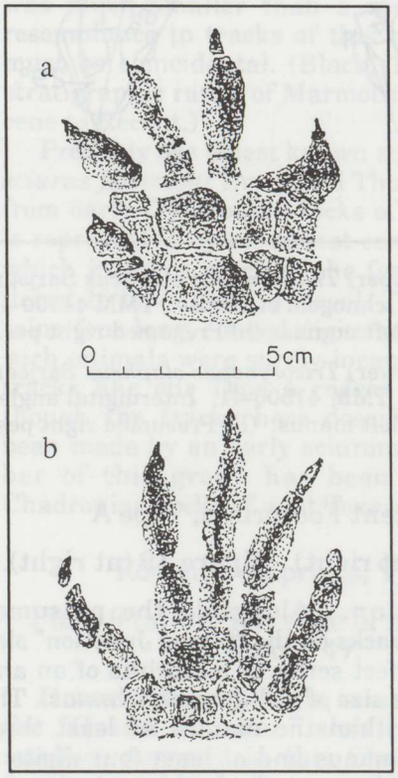
Diagnosis. Very small digitigrade footprints in which only three digits, presumably II to IV, are imprinted. The digits diverge and broaden distally, and bear distinct claws. Manus and pes are closely similar in size.

Type Species. *Tricorynopus elaphrus* Sarjeant and Langston, herein. Late Eocene (Chadronian), west Texas.

Remarks. These footprints are without parallel in the fossil record. Small tridactyl footprints of reptiles are known from the Mesozoic and from present-day sediments, but they do not show any distal thickening of digits—a characteristically mammalian feature. The fact that only three digits were imprinted suggests the animal was running at speed and that the lateral digits (presumably I and V) were held clear of the ground and probably reduced.

It seems unlikely that the trackmaker was bipedal. Apart from the obvious dissimilarity of the fore and hind feet—a dissimilarity too great to be accounted for by foot position during movement—the footprints are quite different from those of the living jerboas and jumping mice, whose footprints are typically semiplan-tigrade to plantigrade and still imprint either four or five much longer digits, even when approaching a digitigrade form (see Murie, 1954, fig. 98).

We attribute these tracks to the Rodentia, rather than to the often equally small (or smaller) shrews (Insectivora) on the grounds



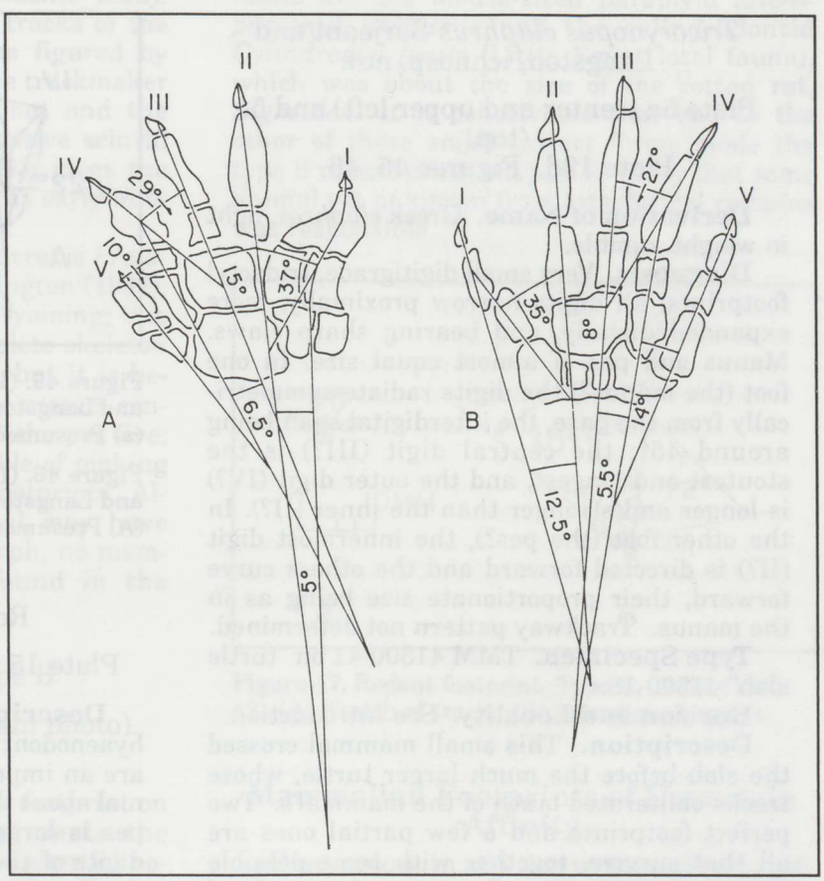


Figure 43.(Left) *Ptyariopus aichmanticheirus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-43. (a) Left manus. (b) Right pes.

Figure 44. (Right) *Ptyariopus aichmanticheirus* Sarjeant and Langston, TMM 41500-43. Interdigital angles. (A) Left manus. (B) Right pes.

that, according to published descriptions (Murie, 1954; Leutscher, 1960), the tracks of shrews are either plantigrade when moving at a moderate to slow pace or digitigrade, with uniformly slender digits, when moving at speed. In contrast, the tracks of small rodents typically show distally expanded digits.

Comparison of *Tricorynopus* with tracks of existing rodents suggests closer affinity with myomorphs than with sciuromorphs. The sciuromorphs tend to be shorter clawed and plantigrade to semiplantigrade, while the majority of myomorphs and *Tricorynopus* are digitigrade. Only one rodent in the west Texas Chadronian may be a myomorph: the systematically enigmatic *?Simimys* sp., from the Porvenir local fauna. The genus is so poorly known that speculation about it as trackmaker is futile. However, other candidates are lacking, since the various Chadronian paramyids, cylindrodontids, ischyromyids, eutypomyids and eomyids were probably either too large or too small to have made the *Tricorynopus* tracks.

Tricorynopus elaphrus Sarjeant and Langston, ichnosp. nov.

Plate 5a (center and upper left) and 5c (top)
Plate 19d. Figures 45, 46.

Derivation of Name. Greek *elaphros*, light in weight, nimble.

Diagnosis. Very small digitigrade, tridactyl footprints; all digits narrow proximally, more expanded distally, and bearing sharp claws. Manus and pes of almost equal size. In one foot (the manus?) the digits radiate symmetrically from the base, the interdigital span being around 45°; the central digit (III?) is the stoutest and longest, and the outer digit (IV?) is longer and stronger than the inner (II?). In the other foot (the pes?), the innermost digit (II?) is directed forward and the others curve forward, their proportionate size being as in the manus. Trackway pattern not determined.

Type Specimen. TMM 41500-41 on "turtle slab" 41500-18.

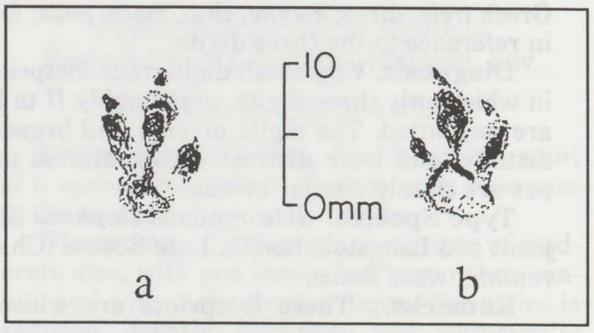
Horizon and Locality. See Introduction.

Description. This small mammal crossed the slab before the much larger turtle, whose tracks obliterated much of the mammal's. Two perfect footprints and a few partial ones are all that survive, together with some possible digit-tip impressions. Consequently, details of trackway pattern and dimensions are not determinable.

Dimensions. Presumed manus: overall length 9 mm, greatest breadth 7.5 mm. Length of digits, as here provisionally identified (fig. 45): II, 5.5 mm; III, 7 mm; IV, 6 mm. Presumed pes: overall length 10 mm, greatest breadth 7 mm. Length of digits: II, 4 mm; III, 6 mm; IV, 5 mm.

Divarication of Digits. See fig. 46 for details.

Remarks. Lacking any clear means for distinguishing them, our identification of manus and pes is arbitrary. For discussion of affinities, see under genus.



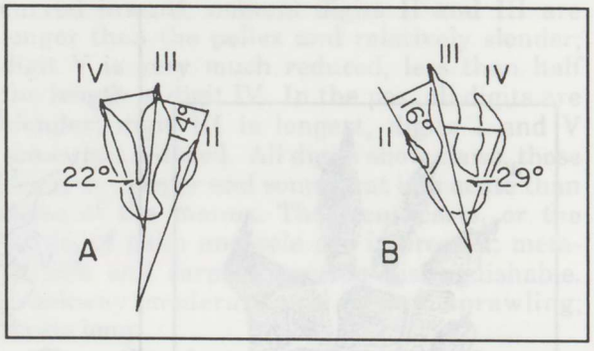


Figure 45. (Upper) *Tricorynopus elaphrus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-41. (a) Presumed left manus. (b) Presumed right pes.

Figure 46. (Lower) *Tricorynopus elaphrus* Sarjeant and Langston, TMM 41500-41. Interdigital angles. (A) Presumed left manus. (B) Presumed right pes.

Rodent Footprints, Type A

Plate 15 (at right). Figure 19 (at right).

Description. Alongside the presumed hyaenodont tracks on the "Grand Junction" slab are an imperfect series of footprints of an animal about the size of a chipmunk (*Tamias*). The pes is larger than the manus. At least three digits of the manus and at least four digits of the pes were impressed, claws not being evident. The manus is digitigrade, the pes semidigitigrade to semiplantigrade. The detail is not sufficient for precise characterization of these tracks, the surface having been slightly

too firm for an animal of such light weight to imprint clear footprints.

Figured Specimen. TMM 41500-39, tracks on section C, position 15 of "Grand Junction" slab (41500-22). Similar prints, even less well preserved, are present also on section D at position 18.

Horizon and Locality. See Introduction.

Dimensions. Breadth of trackway up to 50 mm. Pace ca. 80 mm. Stride ca. 124 mm. Manus: maximum overall length ca. 10 mm, maximum breadth ca. 13 mm. Range of digit lengths ca. 4-7 mm. Pes: maximum overall length ca. 16 mm, maximum breadth ca. 13 mm. Length of digits ca. 8.5-10 mm.

Divarication of Digits. Not accurately measurable. Digits slightly divergent, the interdigital span of the manus (three digits) and of the pes (four digits) being both around 25°.

Remarks. Though of an undescribed type, these tracks are of too low a quality to be named. The character and arrangement of the footprints resembles the pattern seen in walking tracks of ground-dwelling rodents today. They resemble in particular the tracks of the woodchuck (*Marmota monax*), as figured by Murie, 1974, fig. 67f. However, the trackmaker was much smaller than a marmot and the resemblance to tracks of this massive sciurid must be coincidental. (Black, 1963, gives the stratigraphic range of Marmotini as early Miocene to Recent.)

Probably the oldest known squirrel is *Protosciurus jeffersoni* Emry and Thorington (1982), from early Chadronian rocks of Wyoming; this is represented by an almost complete skeleton which includes much of the feet, but it is believed to have been arboreal. The manus contains four long, clawed digits and the pes five; such animals were surely incapable of making tracks like our Type A rodent footprints. Although the tracks here described may have been made by an early sciuromorph, no member of this group has been found in the Chadronian rocks of west Texas.

Rodent Footprints, Type B

Plate 9 (at top left edge of main photo).
Figure 47.

Description. A single, minute footprint on the "Grand Junction" slab represents the smallest mammal in this Chadronian ichnofossil assemblage. It is semidigitigrade and tetradactyl (probably digits I to IV) One digit, presumably I, shows a degree of opposition, the others being more narrowly spaced; the total interdigital span approaches 130°. The digital pads are petaloid in shape, and distinct impressions of at least three metacarpals (or metatarsals?) are visible.

Figured Specimen. TMM 41500-42, close to bird footprints (*Avipeda* aff. *phoenix*) on Section D, "Grand Junction" slab (TMM 41500-22).

Horizon and Locality. See Introduction.

Dimensions. Overall length 8 mm, greatest breadth 9.5 mm. Length of digits, as here identified (fig. 47, at right): I, 3 mm; II, 3.5 mm; III, 2.5 mm; IV, 3.5 mm.

Divarication of Digits. See fig. 47, at right, for explanation.

Remarks. This single footprint differs from the digitigrade footprints of shrews in exhibiting digital pads (compare Murie, 1954, fig. 4i) and thus resembles the footprints of mice, in which claws are not impressed (see Murie, op. cit. fig. 101e). It is clearly of a type yet unreported from the Tertiary, but our information is too scant for any new name to be proposed.

The smallest rodents in the Porvenir local fauna are the mouse-sized paramyid *Microparamys perfossus* and the cylindrodontid *Cylindrodon fontis* (Little Egypt local fauna), which was about the size of the cotton rat, *Sigmodon*. It is conceivable that one or the other of these small extinct forms made the type B rodent print, but just as likely that some animal yet unknown from osteological remains was responsible.

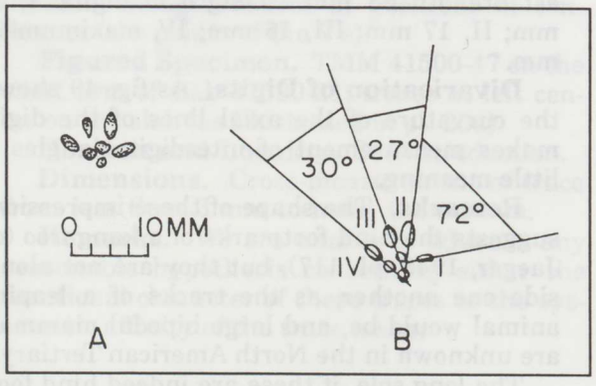


Figure 47. Rodent footprint, Type B, TMM 41500-42. (A) Sketch of track. (B) Interdigital angles.

Mammalian Footprints of Uncertain Affinity

Discussion. In addition to the eighteen footprint types described above, others are present on the "Electric Guitar" slab that, although capable of clear characterization, are of such puzzling nature as to defy systematic assignation. These are described below.

On the "Grand Junction" slab there are also several other footprints whose preservation, either because they were emplaced on a surface too dry or too wet to preserve detail or as a consequence of such post-diagenetic effects as jointing or surface flaking, do not reflect pedal morphology sufficiently well to merit description. These have been left undescribed.

Mammalian Footprints, Type A

Plate 11. Plate 12a. Figures 48, 49.

Description. Two plantigrade footprints on the "Electric Guitar" slab—one of them (LP_1: see pl. 11) overprinting an earlier footprint and affected by cracking, the other quite well preserved (RP_1: see pl. 11 and pl. 12 fig. 1)—are longer than any other traces in the collection. The animal's weight was, it seems, taken on the front part of the sole (or palm?); the four digits are lightly impressed and occupy only one-fifth of the footprint's length. The four blunt nails (presumably I to IV) are directed outward, I and II curving slightly and III being rather square. Trackway narrow; pace (and, presumably, stride also) quite long.

Figured Specimens. TMM 41500-44 on "electric guitar" slab (TMM 41500-15).

Horizon and Locality. See Introduction.

Dimensions. Breadth of trackway 87.5 mm; pace 280 mm; stride not measurable. Overall length of presumed pes 92 mm, greatest breadth 53 mm. Length of digits: I, 22 mm; II, 17 mm; III, 16 mm; IV, maximum 24 mm.

Divarication of Digits. As fig. 49 shows, the curvature of the axial lines of the digits makes measurement of interdigital angles of little meaning.

Remarks. The shape of these impressions suggests the hind footmarks of a kangaroo (cf. Jaeger, 1948, pl. 117), but they are not alongside one another, as the tracks of a leaping animal would be, and large bipedal mammals are unknown in the North American Tertiary.

The long sole, if these are indeed hind footprints, is reminiscent of monkey tracks (cf. Jaeger, op. cit., pl. 101), but no monkeys are known from the North American Tertiary. Some other primates are well represented in

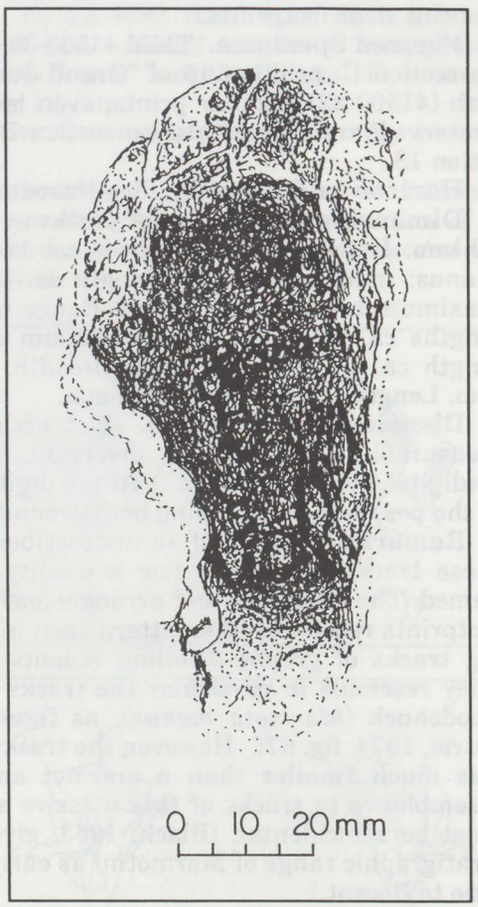


Figure 48. (Top) Vertebrate footprint of undetermined affinity, Type I, TMM 41500-44 (probably the right pes).

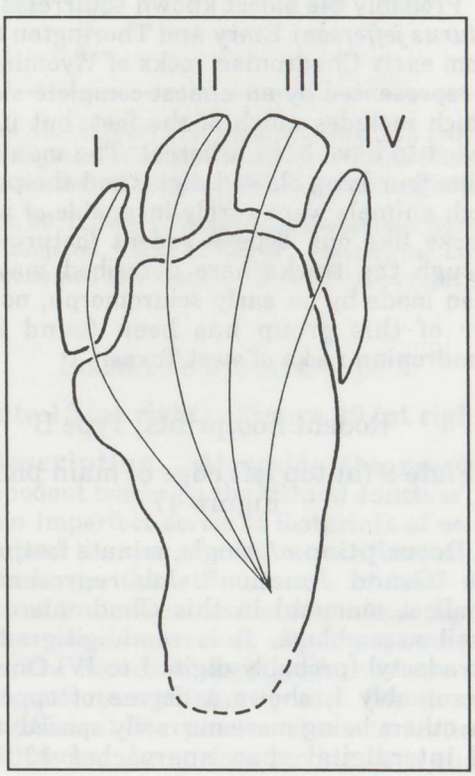


Figure 49. (Bottom) Vertebrate footprint of undetermined affinity, Type I, TMM 41500-44 (probably the right pes). Interdigital angles.

the Paleogene of the region and one genus, *Rooneyia*, occurs in the Porvenir local fauna (see Wilson, 1977, 1986). However, it seems unlikely that the diminutive *Rooneyia* had such large feet and long stride as these tracks indicate.

The number of digits might suggest an artiodactyl, but they are so lightly impressed that they can scarcely be viewed as hooves; moreover, so long a palm or sole appears improbable in an artiodactyl. We are thus unable to suggest any animal that might have made these tracks.

II. INVERTEBRATE TRACES: Introduction

Invertebrate traces are seen on the "Grand Junction" slab, but they are too indistinct and incomplete for description. The two types described below are from another, much smaller slab. Both present problems in interpretation, but their description for the record seems appropriate.

Invertebrate Trace, Type A

Plate 25a-c. Figure 50.

Description. This trackway consists of two rows of invertebrate footprints on either side of a broad central space. The footprints of the inner rows are larger and more distinct than those of the outer rows and are of irregular shape (see fig. 50). In each row, the spacing of the footprints is close but irregular.

Figured Specimen. TMM 41500-46 on the short arm of slab 41500-21; traces running the whole length of the slab.

Horizon and Locality. See Introduction.

Dimensions. Total breadth of track 11.5 mm; space between inner tracks 6 mm. Average length of inner, larger footprints ca. 2 mm, maximum breadth ca. 1.25 mm. Average length of outer, smaller footprints ca. 1.25 mm, maximum breadth ca. 0.5 mm.

Remarks. The most similar described tracks are to be found among the range of invertebrate traces included in the genus *Protichnites* Owen (see Häntzschel, 1975:W97, fig. 61). This taxon accommodates not only trilobite tracks, but also the tracks of several groups of crustaceans. However, in *Protichnites* there is a narrow double-drag trail intermittently to be seen at the center between the footprint lines. These Texas tracks show no such feature at any point in the whole 42 cm length of the impression. The trackmaker evidently carried its body well clear of the ground. It seems evident that it was a multi-limbed arthropod of some kind; but we cannot be more explicit.

Invertebrate Trace, Type B

Plate 25a-d. Figure 51.

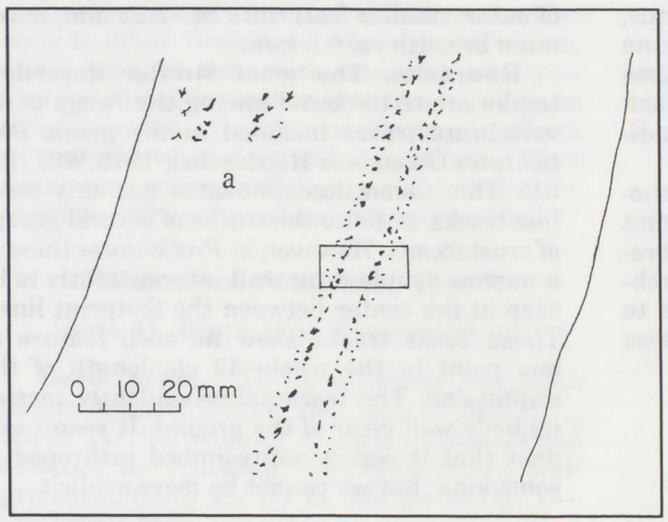
Description. These traces are seen at the side of the same slab and are even more puzzling. They are arranged in tracks forming a sort of narrow double V, whose two ends open in opposite direction. Examined in detail, these tracks each show two sorts of fine lines—longer, irregularly trifid ramose or arboriform lines, their expanded ends in close proximity, and between their bases one to four much shorter lines, simple or variably bifid, solid or broken. The tracks vary considerably in relative breadth, being broadest at positions of confluence (the points of the V's).

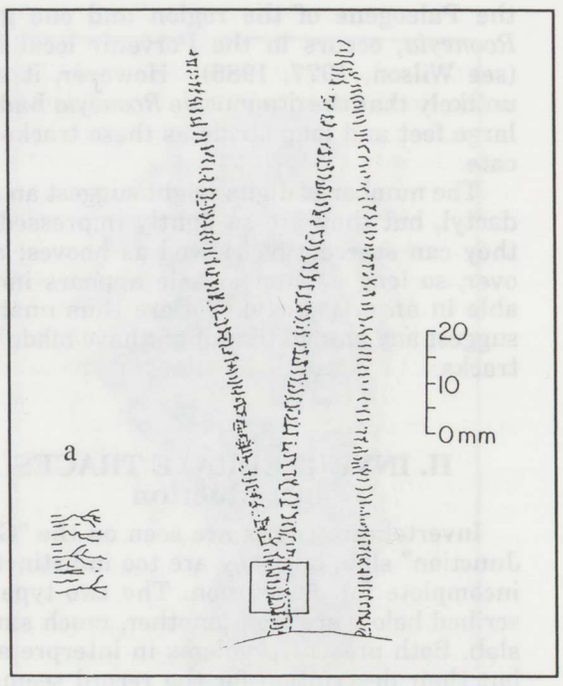
Figured Specimen. TMM 41500-47 on the short arm of slab 41500-21; traces at left center on the slab (as illustrated in pl. 25a).

Horizon and Locality. See Introduction.

Dimensions. Cross-measurement of trace from less than 3 mm to more than 4 mm.

Remarks. We are unable to advance any reasonable hypothesis concerning either the functional character of these traces or the systematic affinity of the trace maker.





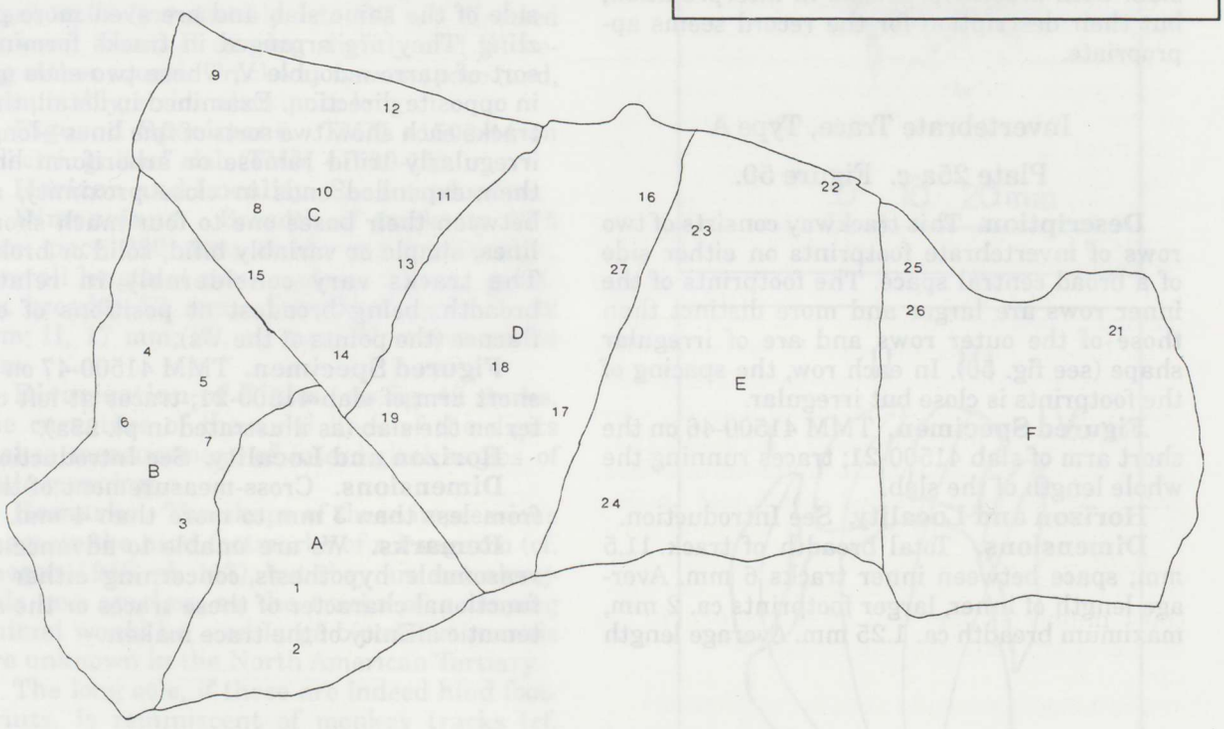


Figure 50. (Top left) Invertebrate traces, Type A, TMM 41500-46. (a) Enlarged detail of the section enclosed within box.

Figure 51. (Top right) Invertebrate traces, Type B, TMM 41500-47. (a) Enlarged detail of the section enclosed within box.

Figure 52. (Above) Plan of the "Grand Junction" slab, TMM 41500-22, with numbers indicating the position of footprints, or footprint groups, that were studied in detail. (Not all are described herein: other numbers are included to facilitate future reference to the authors' notes and photographs). The whole slab is shown on Plate 4.

CONCLUSIONS

This is the richest ichnofauna yet discovered in the North American Tertiary and perhaps the richest to be found in post-Mesozoic strata. Indeed, only the ichnofaunas described from the Miocene of western Ukraine by O. S. Vialov (1965, 1966) and of Hungary by S. Kordos (1983) show a comparable diversity of morphotypes; and these are of much later date, subsequent to the faunistic overturn caused by the spread of the grasses. The casts in the Texas Memorial Museum collections afford an excellent basis for the study of this remarkable footprint assemblage.

Although fine details of even very small tracks are sometimes preserved—indeed, two very fine traces of invertebrates are present—no amphibian or lizard tracks have been identified. Reptile tracks are limited to two kinds of turtle tracks: one (*Chelonipus chadronicus*) of moderate size was an inefficient pedestrian, the other (*C. parvus*) of smaller size was more agile.

Five types of bird tracks are present. Two (*Fuscinapeda texana* and *Fuscinapeda?* sp.), probably made by wading birds, are quite large, but most are small. Of the small tracks, one type (*Gruipeda calcarifera*), is probably that of a rail; the others (*Avipeda adunca* and *Avipeda* cf. *A. phoenix*) are too generalized in character to permit confident identification. Despite these uncertainties, the avian footprints are of particular interest because osteological remains of birds have not been reported from either the late Eocene or the early Oligocene of west Texas (see Wilson, 1978, 1986 for faunal lists).

The greatest interest of this ichnofauna lies, however, in its abundant mammalian foot prints. As has been stressed earlier (pp. 18-19), the paucity of osteological information concerning the foot structure, and in particular the character of the phalanges, in many Tertiary mammals has caused us considerable problems in identifying the trackmakers. At the same time, the novel details of pedal morphology cataloged here add greatly to the interest of the assemblage. If new information on pedal osteology is forthcoming, these footprints will be a valuable supplement, furnishing details of pads and claws that could never be ascertained from bones alone. Moreover, by showing the manner of movement, the footprints furnish information on the behavior of long-vanished mammals that can be gained from no other source.

Many of our identifications are provisional, and we have taken care to use descriptive names, rather than names that imply a particular affinity, in naming new ichnogenera and species. (For the problems that can be caused by the converse procedure, see p.41). The identifications are based on skeletal morphology, where known; on modern analogues; and on the available osteological information on west Texan Chadronian faunas, as indicative of the region's population at that time. In all instances, we have given reasons for our inferences concerning possible trackmakers and have striven to distinguish between strong evidence and mere speculation.

If our identifications are correct, the Late Eocene mammalian fauna includes an insectivore (*Schyromorphipus oxypages*), about as large as a domestic cat; a creodont (*Zanclonychopus cinicalcator*); five carnivores, of which one (*Tetrastoibopus phoros*) surely, and another (*Falcatipes floriformis*) probably, are miacids (*Phacelopus therates*), one a likely mustelid (*Phacelopus therates*) and two amphicyonids (*Axiciapes ferox* and *A. curvidigitatus*); a mesonychian (*Corymbipes superstes*); three perissodactyls, comprising a tapiroid (*Apoxypus tessellatus*), a rhinocerotoid (*Thrinaxopus hoplephoreus*) and a very large animal, either a brontothere or an amynodont; two artiodactyls, one probably an entelodont (*Anoplotheriipus zeuctus*) and the other a cameloid (*Gambapes hastatus*); four rodents, including an ischyromyid (*Ptyariopus aichmanticheirus*) and a remarkable tridactyl track (*Tricorynopus elephrus*); and two problematica, one possibly either a clawed perissodactyl or a creodont (*Palimmecopus praecursor*) and the other of wholly problematic affinity.

The most noteworthy features of this ichnological assemblage are the high proportion of carnivorous mammals—one-third of the described morphotypes—and the absence of a number of types of ungulates—horses, traguloids, agriochoeres and merycoidodonts—known from osteological remains in the west Texas Chadronian. Among the most probable explanations for these absences, if they are not fortuitous, are differences in precise habitat and seasonal migrations. In contrast, it is hard to advance good reasons for the abnormally high proportion of flesh-eaters, a characteristic of

entrapment situations of which there is no direct evidence.

Also of interest is the fact that, though some of the bird tracks have a pattern suggesting a search for food, the mammals seem to have been moving purposefully, neither pursuing prey nor lingering to graze or rest. It seems likely that the surface of freshly fallen ash afforded scant plant food for the herbivores, while the lack of any inducement for herbivores to linger would not have made prey available to the carnivores. In general, however, the ichnofauna shows a satisfactory accord with the osteological record from Chadronian Trans-Pecos Texas, as described by Wilson (1978). Moreover it presents us, for the first time, with a picture of those animals in action.

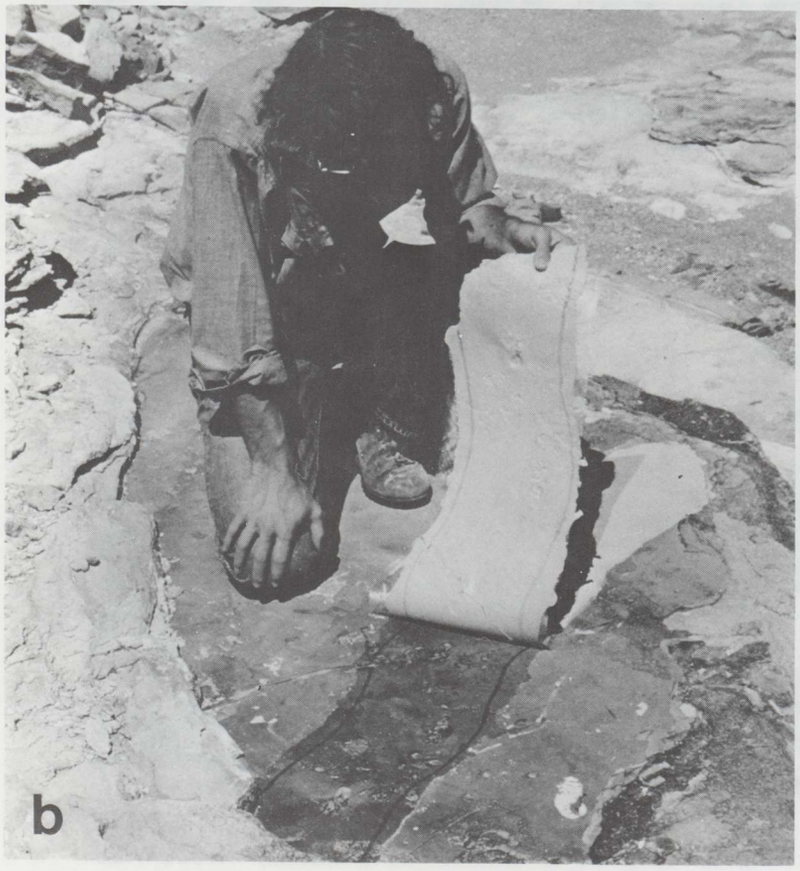


Plate 1. Vertebrate footprints in an outcrop of late Eocene tuff, Presidio County, Texas. (a) Part of the "Grand Junction" slab (TMM 41500-22); natural rock surface of section D at left, Smooth-On mold of section C at right (see pl. 4 for key to the "Grand Junction" slab).
(b) Peeling off a mold of mammalian tracks, used later to cast slab TMM 41500-16. (Photos: J. A. Wilson)

Plate 2. Molds of the Presidio County footprints. (a) A large mold being carried from the outcrop on a stretcher. (Photo: R. H. Rainey) (b) Painting the molding compound onto the "Grand Junction" slab. (Photo: J.A. Wilson)

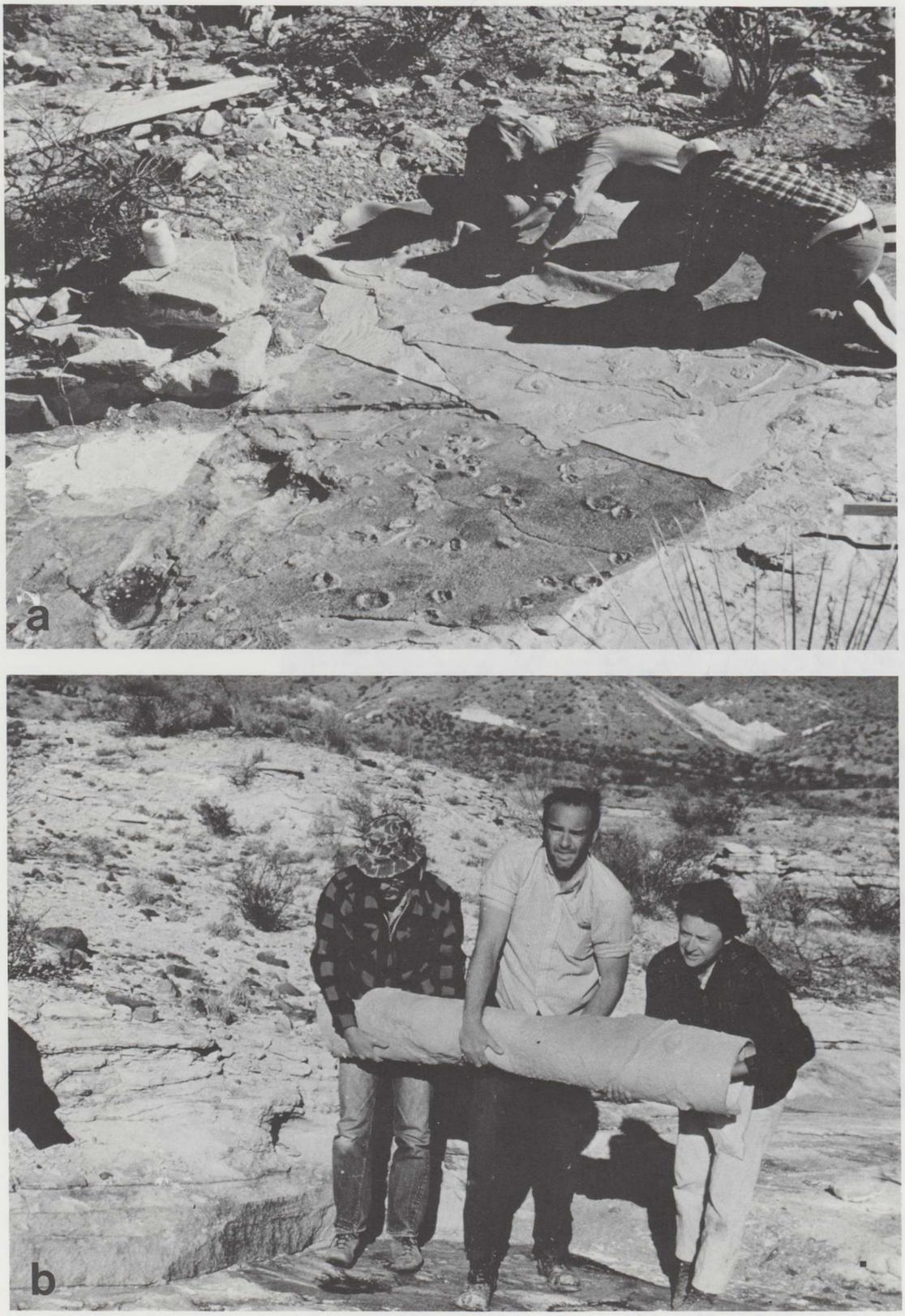


Plate 3. Molds of the Presidio County footprints. (a) A mold of part of the "Grand Junction" slab being peeled off the rock surface. (b) A rolled-up mold being carried from the outcrop. (Photos: J. A. Wilson)

Foldout for Plate 4.

Plate 4. The assembled casts of the "Grand Junction" slab (TMM 41500- 22), with its many criss-crossing trails of mammals and birds. The slab measures approximately 2.7 m x 5.5 m. Inset: Key to the numbering of the six indi-vidual casts. The position of the particular footprints, or footprint groups, referred to in the text, are shown on fig. 52.

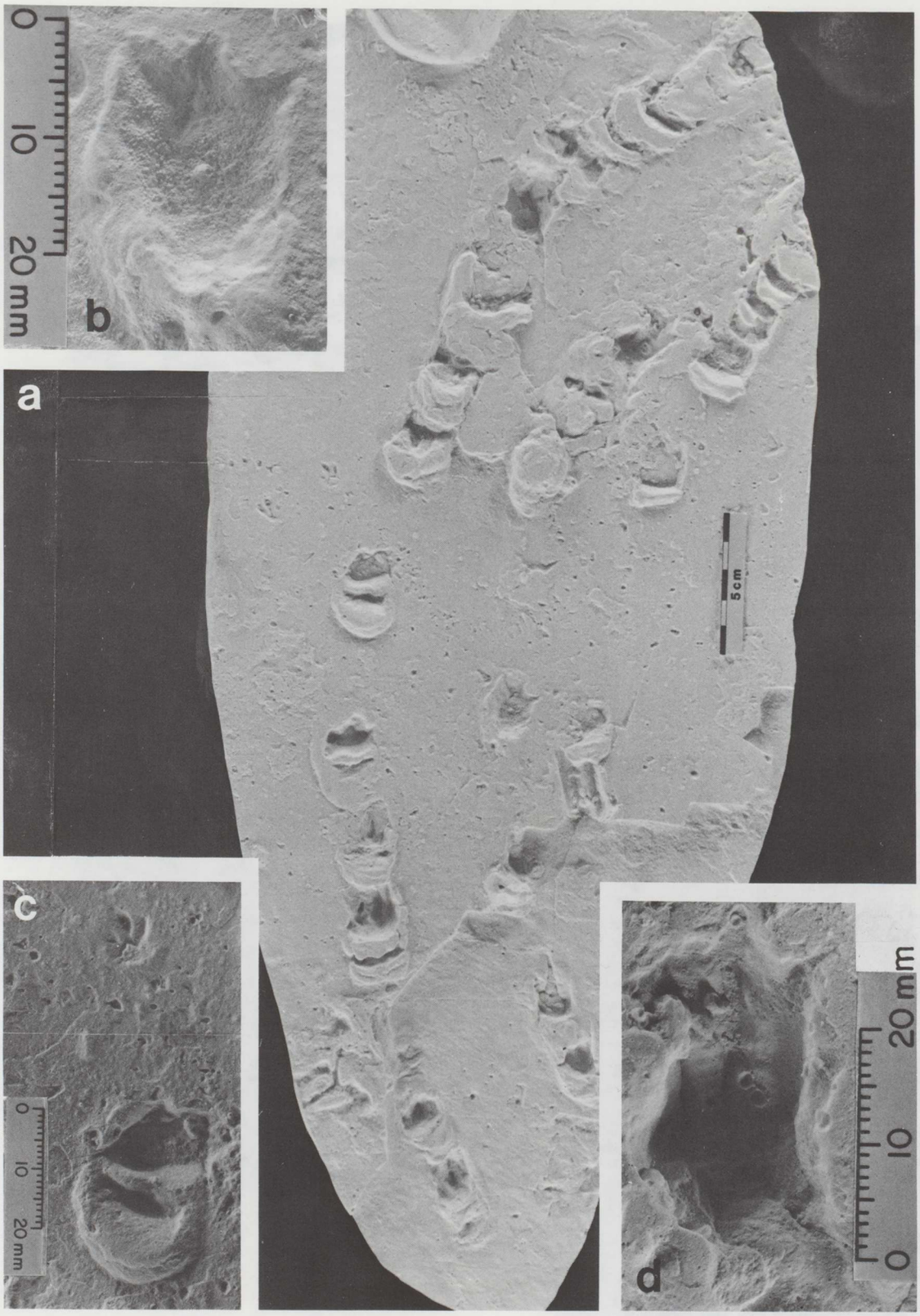


Plate 5. Turtle tracks (*Chelonipus chadronicus* Sarjeant and Langston, ichnosp. nov., TMM 41500-40) (a) Whole trackway. (b) Right manus. (c) Left manus: impression marred by mud adherent to palm. (d) Right pes at top, superposed on an earlier manus impression. Small mammal footprint impressions (*Tricorynopus elaphrus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-41) may also be seen at center and left in (a) and at top of (c).

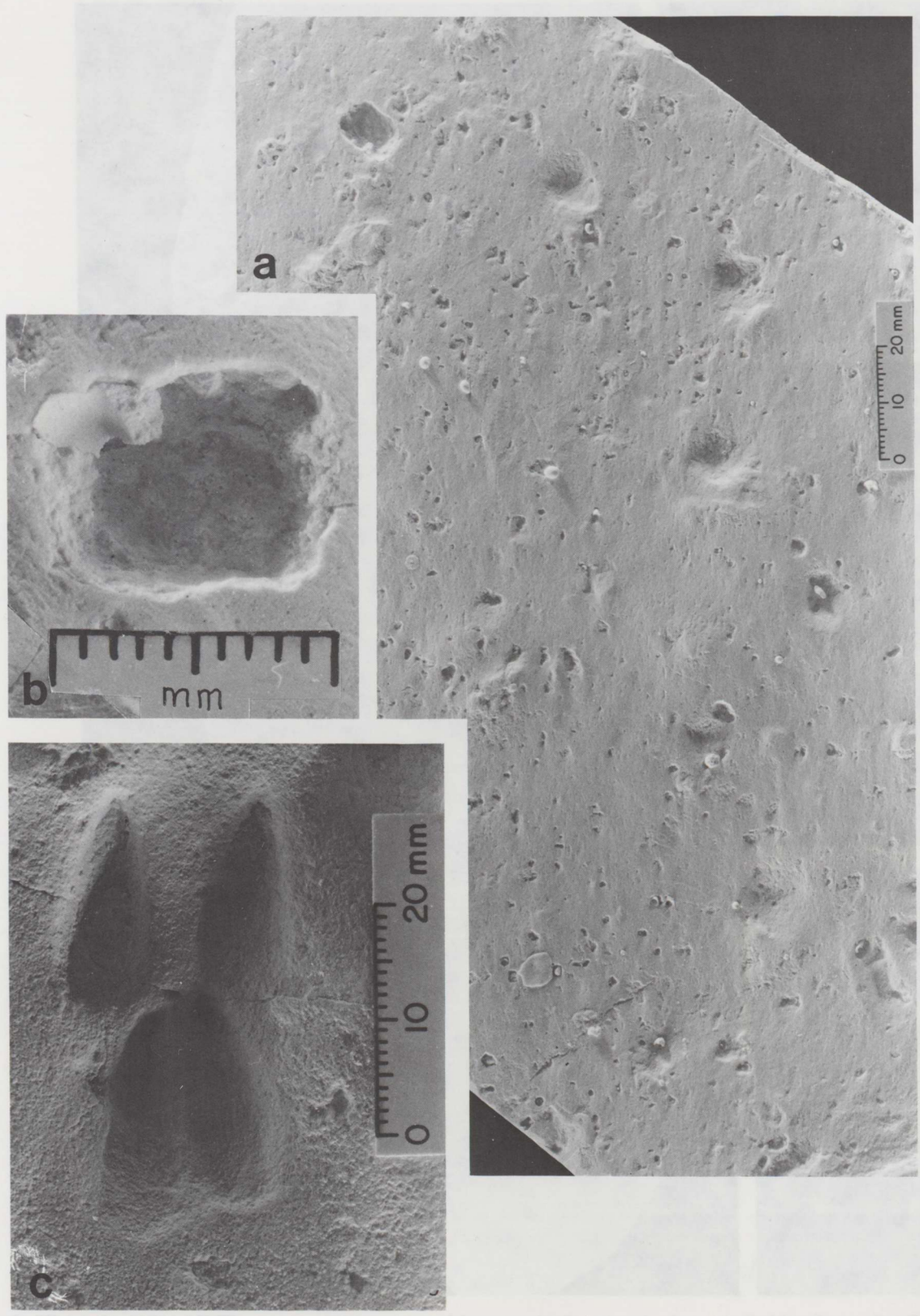


Plate 6. a-b. Turtle tracks (*Chelonipus parvus* Sarjeant and Langston, ichnosp. nov., TMM 41500-23). (a) Whole trackway. (b) Pes, enlarged. (c) Tylopod or pecoran hoofprints (*Gambapes hastatus* Sarjeant and Langston, ichnosp. nov., TMM 41500-20), with pes placed ahead of manus.

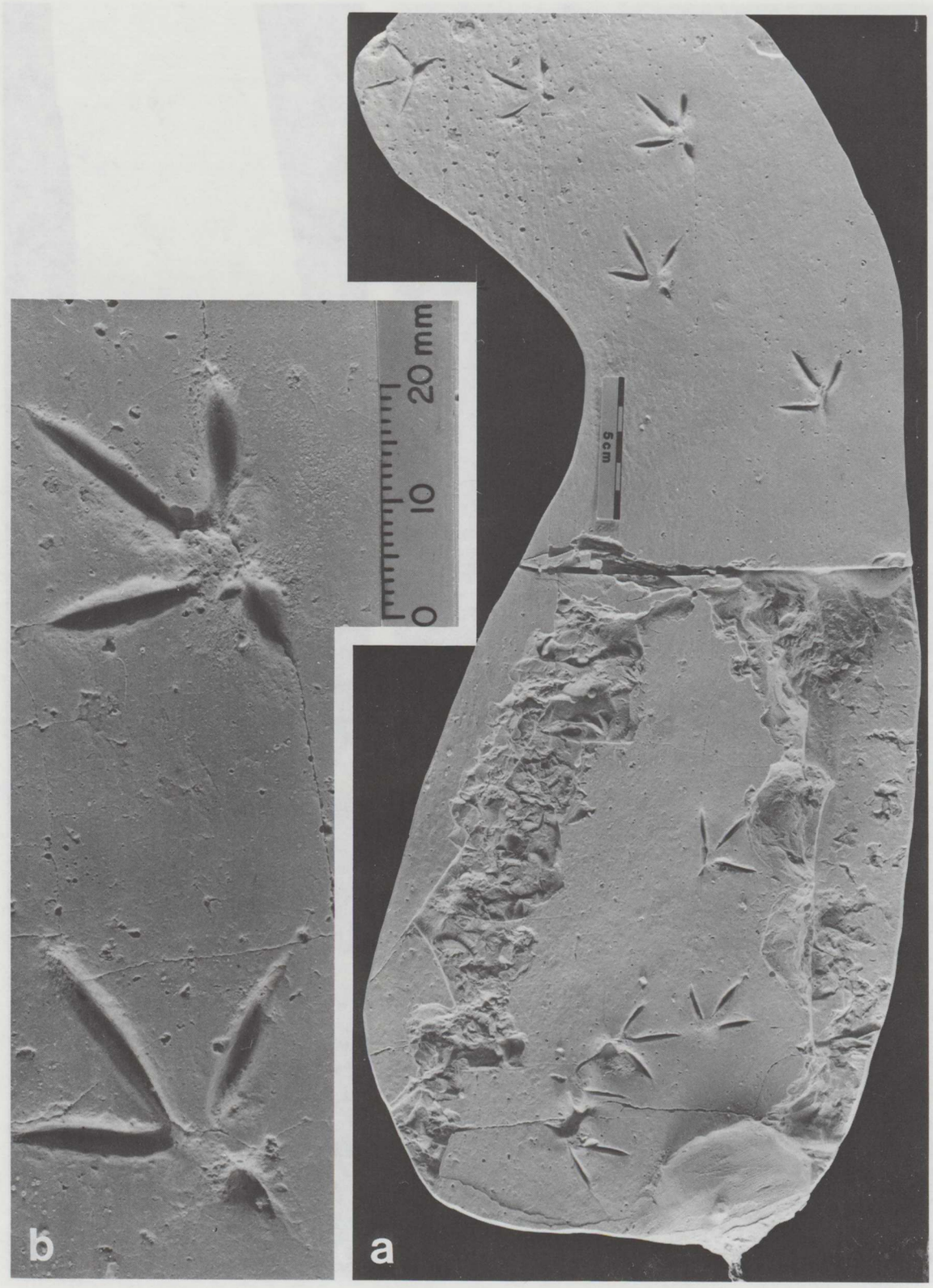


Plate 7. Bird tracks (*Gruipeda calcarifera* Sarjeant and Langston, ichnosp. nov., TMM 41500-19). (a) Whole slab. (b) Two prints, enlarged.

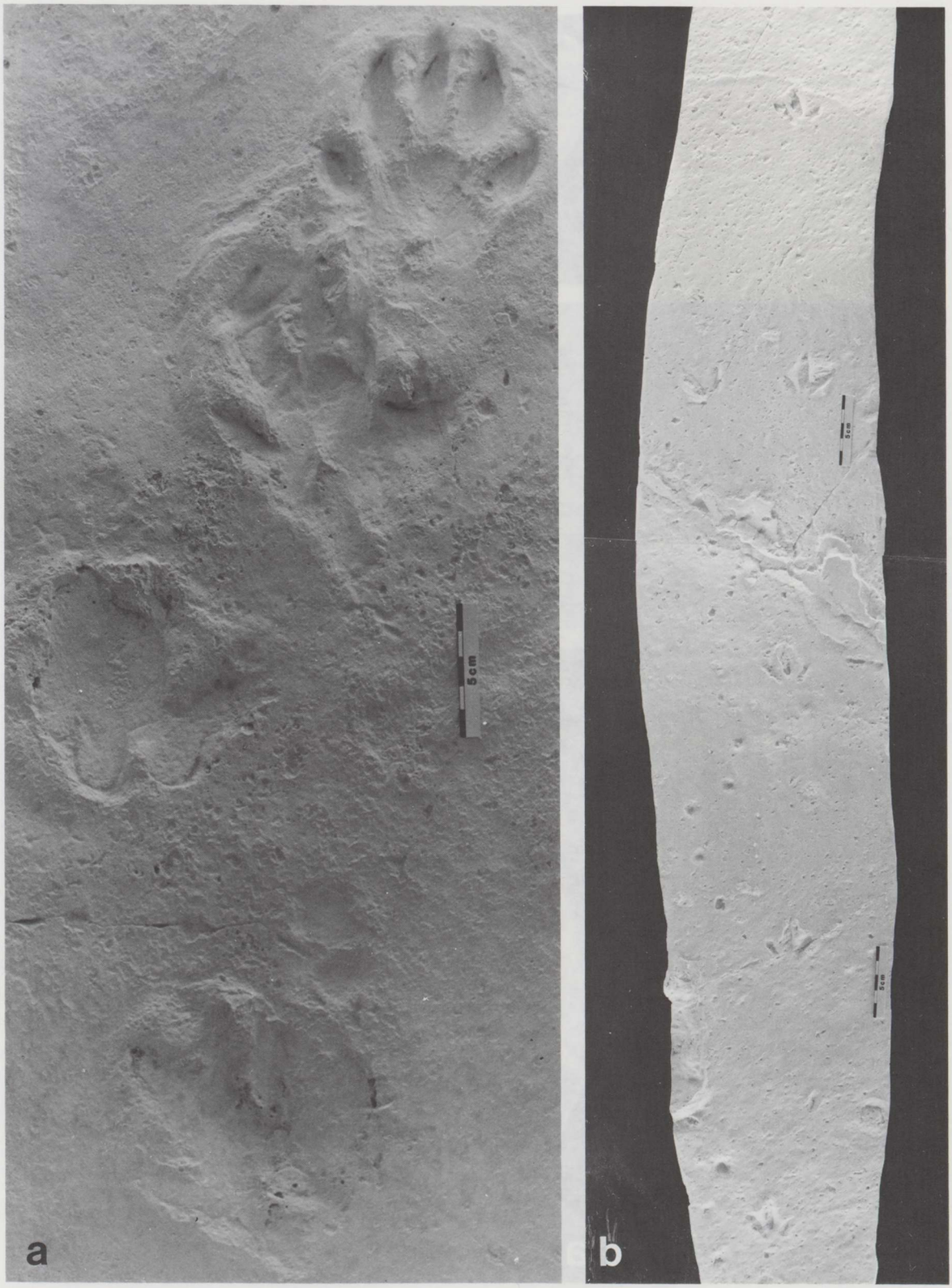


Plate 8. (a) Tracks of a carnivore, probably a primitive mustelid (*Phacelopus therates* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-32). (b) Bird tracks (*Avipeda adunca* Sarjeant and Langston, ichnosp. nov., TMM 41500-24).

Plate 9. Bird tracks (*Avipeda* aff. *A. phoenix* Vialov, TMM 41500-25). Main track at low magnification. The letters [a'-c'] identify the imprints enlarged as a-c. The footprint of a small mammal (rodent footprint type B, TMM 41500-42) may be seen just above and to the right of b'.

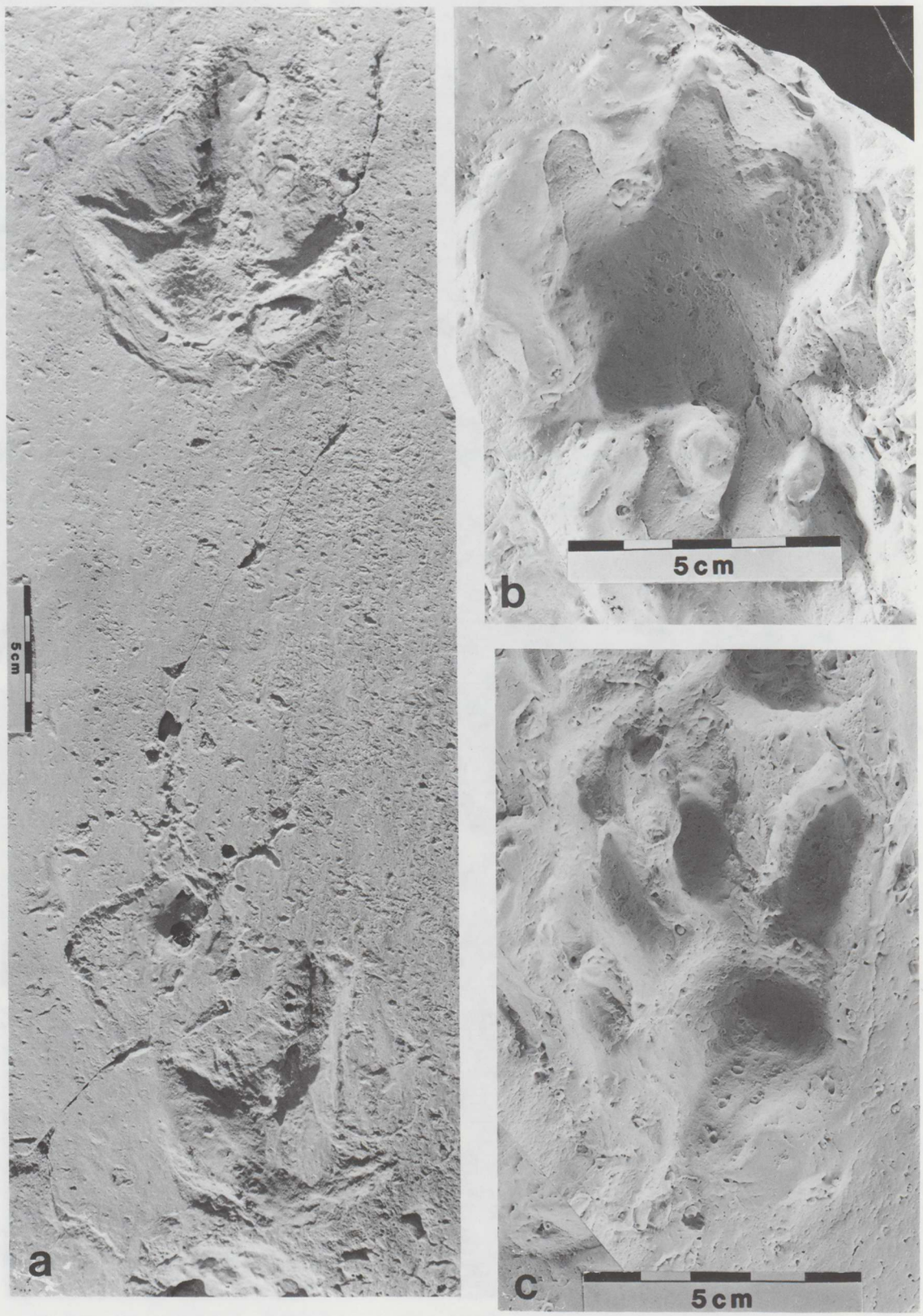


Plate 10. (a) Tracks of a large bird (*Fuscinapeda texana* Sarjeant and Langston, ichnosp. nov., TMM 41500-26). (b-c) Footprints of a canid (*Axiciapes ferox* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-13). (b) Right manus. (c) Left pes.

Foldout for Plate 11.

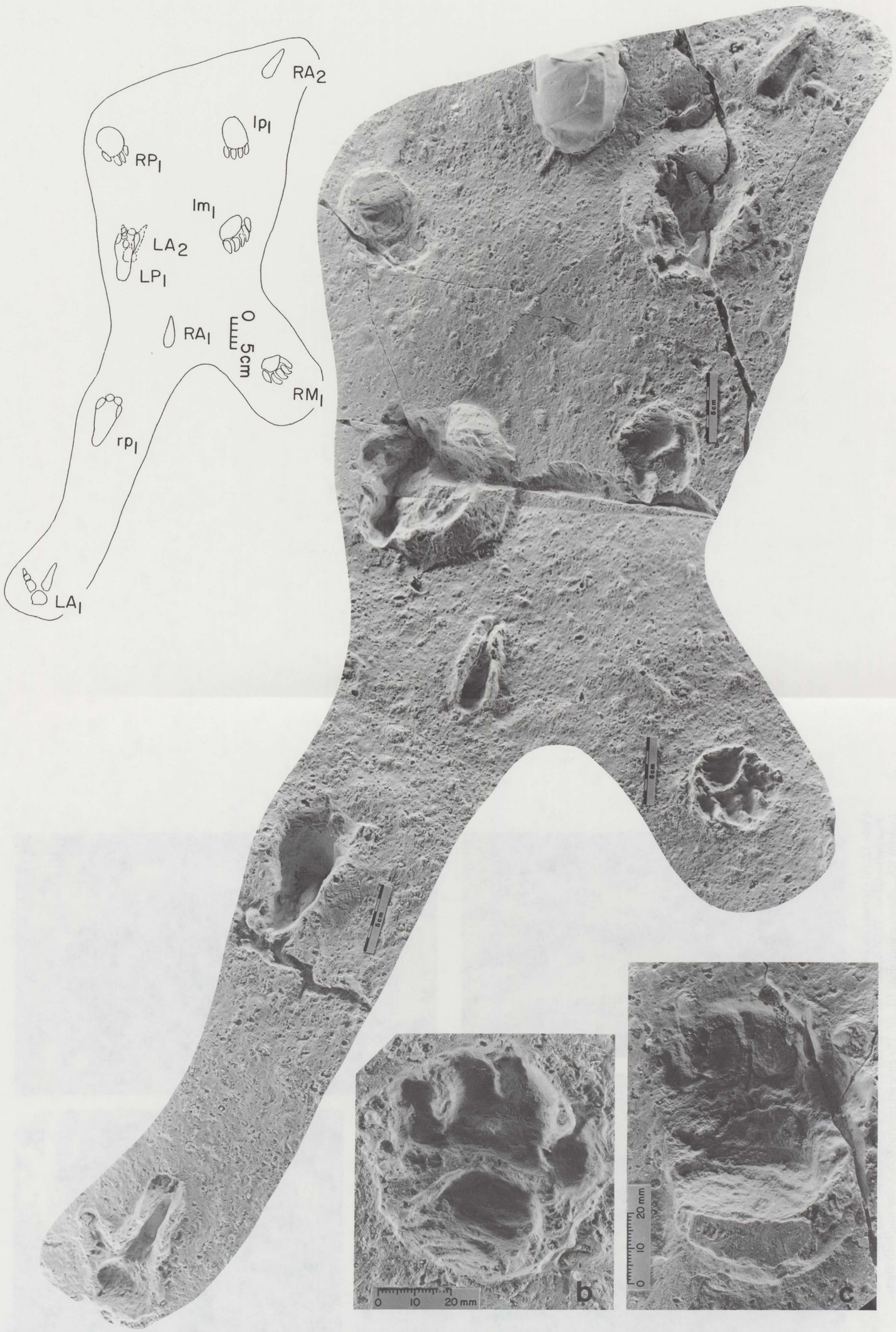


Plate 11. "Electric guitar" slab (TMM 41500-15), showing tracks of a bird and two mammals. In the inset, the bird tracks (*Fuscinapeda?* sp., TMM 41500-27) are indicated by $RA_{1\text{-}2}$ and $LA_{1\text{-}2}$ and the footprints of a mammal of undetermined affinity (Type I, TMM 41500-44) by RP_1 and LP_1. Tracks of a carnivore (*Axiciapes curvidigitatus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-33), moving in the contrary direction, are shown by lower-case letters. (b) and (c) show the right manus and right pes, respectively, of *A. curvidigitatus*.

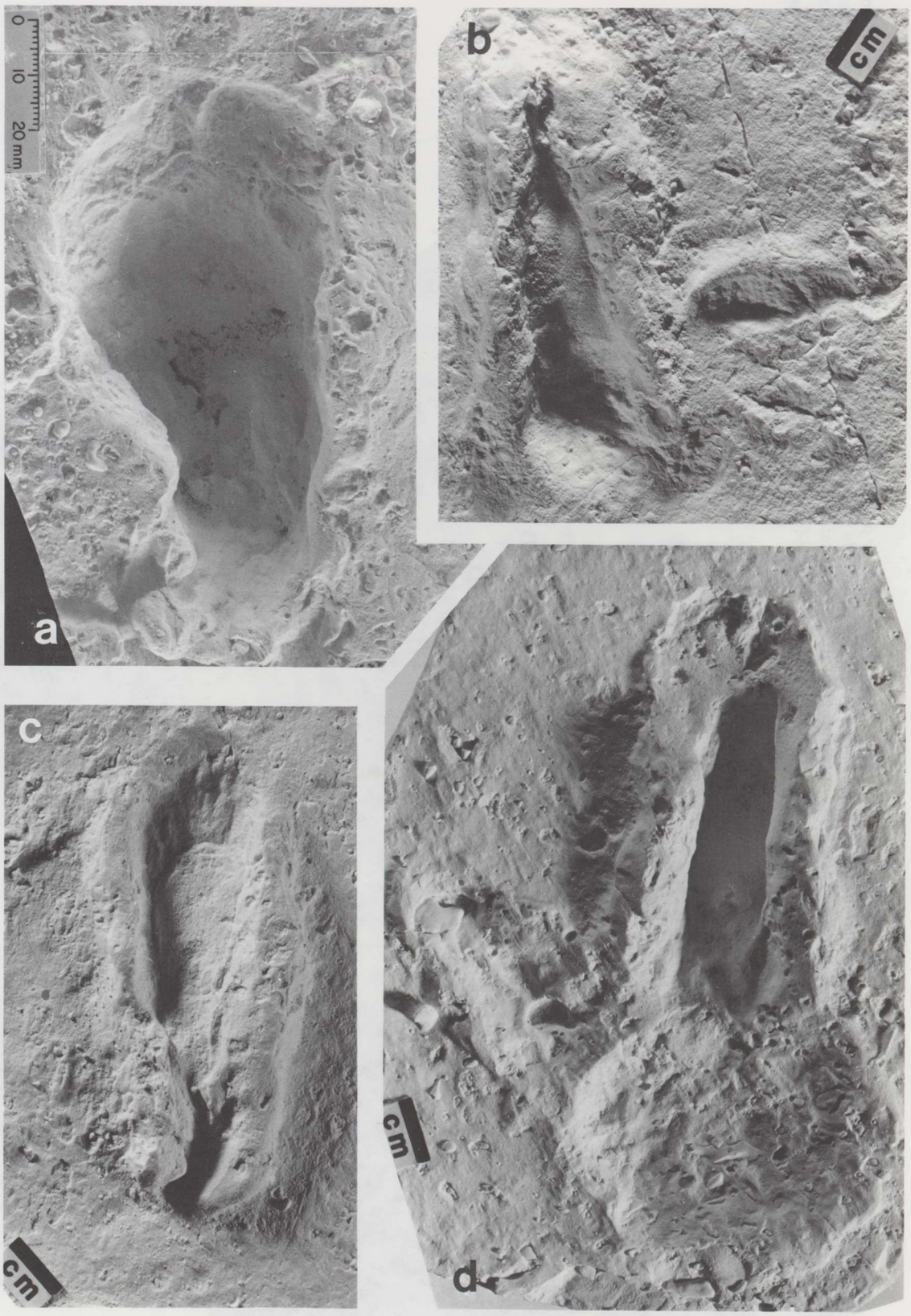


Plate 12. (a) Vertebrate footprint of undetermined affinity (Type I, TMM 41500-44). (b-d) Presumed bird tracks (*Fuscinapeda?* sp., TMM 41500-27). (b) Imprint RA_2, with digit IV partially filled by back-flow of mud. (c) Imprint RA_1, showing only digit III. (d) The clearest imprint (LA_1), showing both digits.

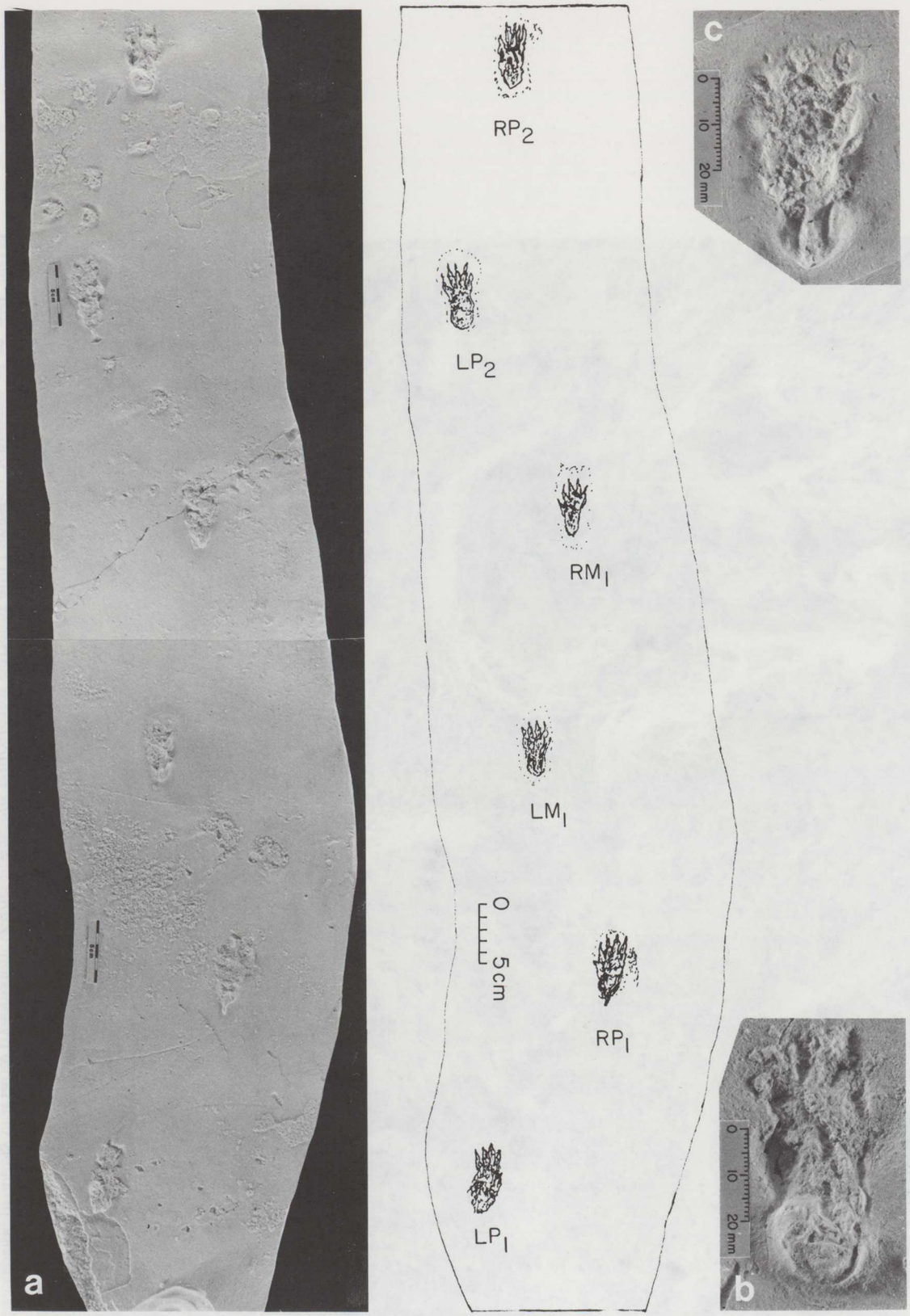


Plate 13. Presumed insectivore tracks (*Schyromorphipus oxypages* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-16). (a) The whole trackway. (b) Left manus (LM_1), enlarged. (c) Right pes (RP_2), enlarged.

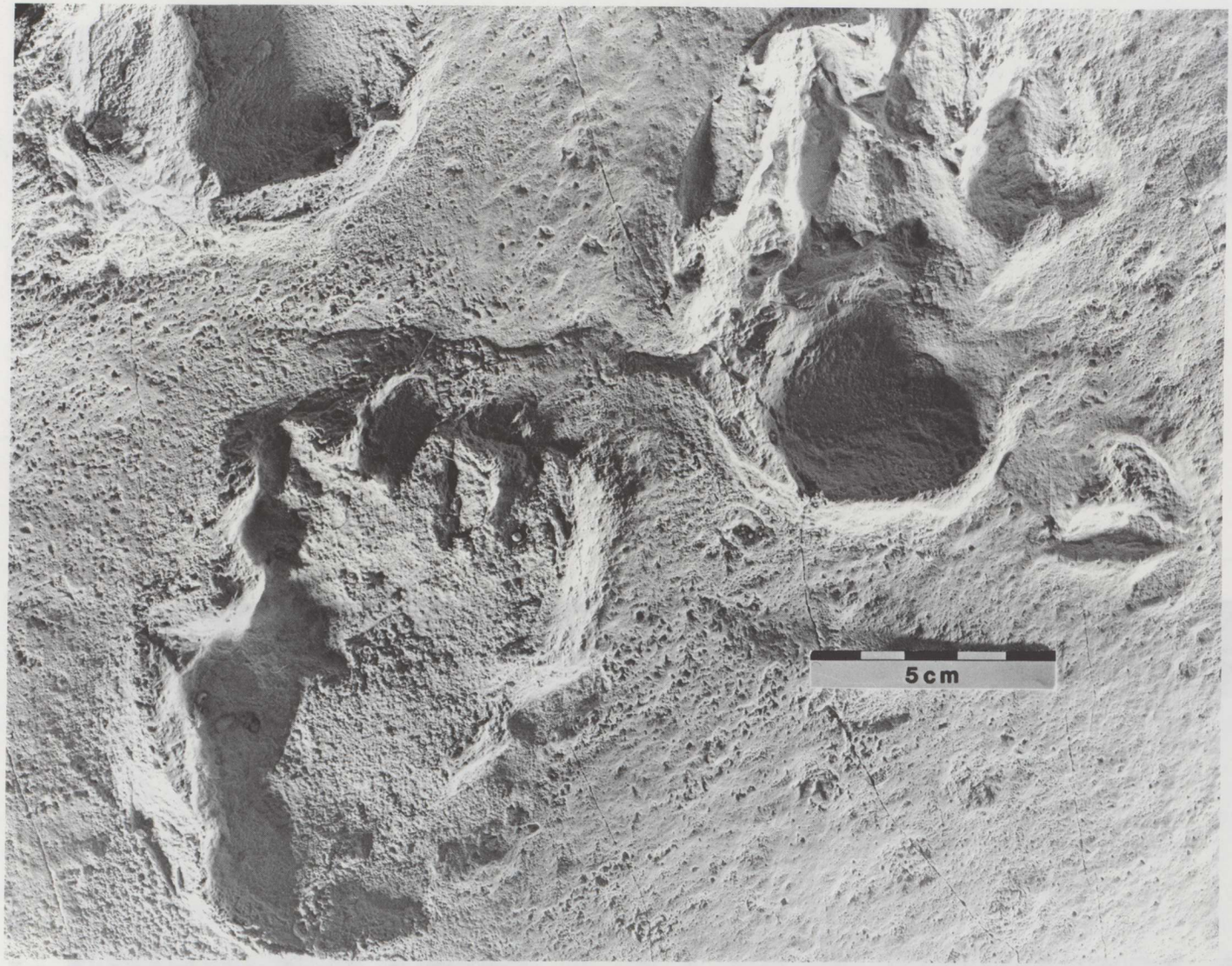
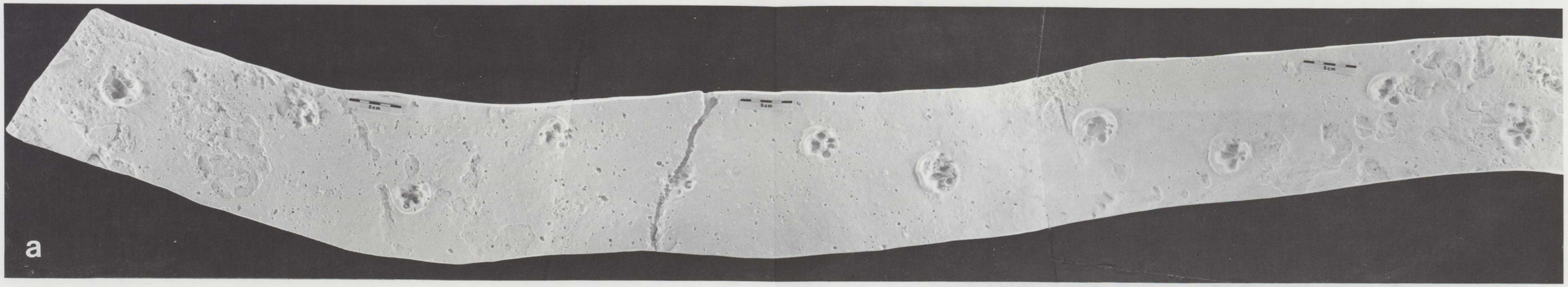
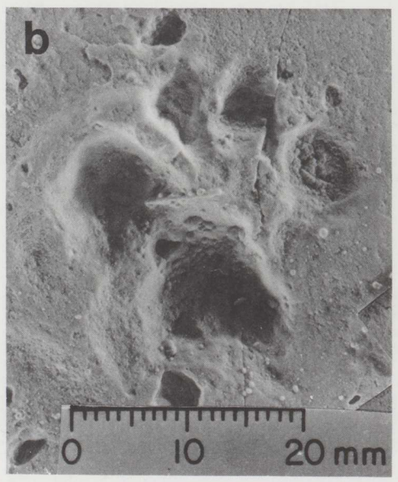


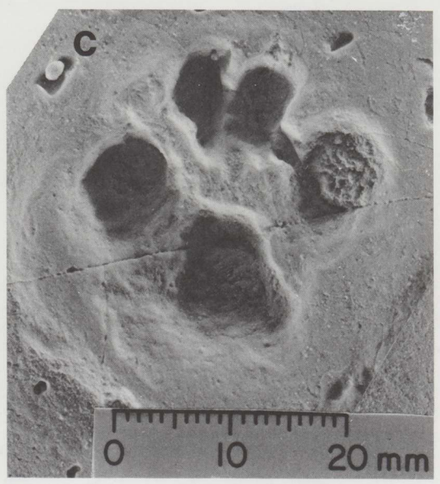
Plate 14. Tracks, probably of a large hyaenodont (*Zanclonychopus cinicalcator* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-28). Holotype, with left manus at lower left and left pes at upper right. A bird footprint (*Avipeda* aff. *phoenix* Vialov, TMM 41500-25) is seen at right.

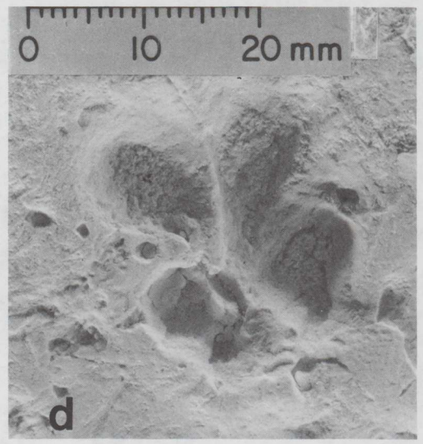
Plate 15. Tracks, probably of a juvenile hyaenodont (*Zanclonychopus cinicalcator* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-29) at left and tracks of a small mammal, probably an ischyromyoid rodent (rodent footprint type A, TMM 41500-39) at right.

Foldout for Plate 16.









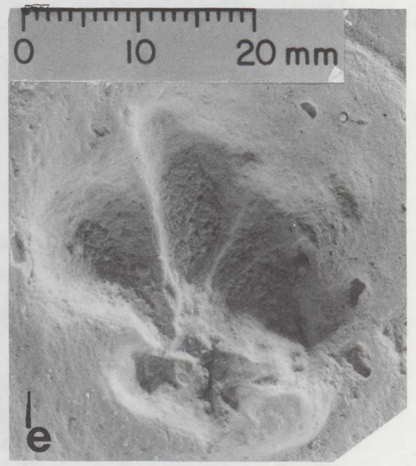
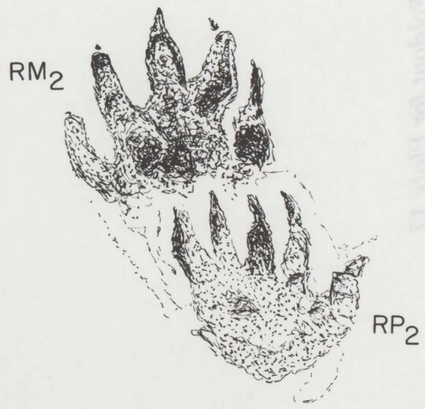
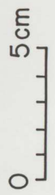
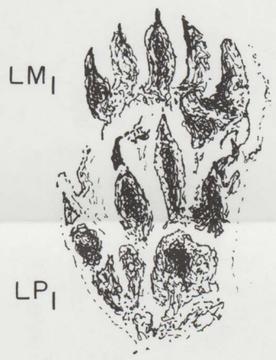


Plate 16. (a) Trackways of two small carnivores, approaching respectively from right and left and sidestepping at encounter (slab TMM 41500-21). At left and in (b) and (c), *Tetrastoibopus phoros* Sarjeant and Langston, ichnogen. et sp. nov. (TMM 41500-30). At right and in (d) and (e), *Falcatipes floriformis* Sarjeant and Langston, ichnogen. et sp. nov. (TMM 41500-31).

Foldout for Plate 17.







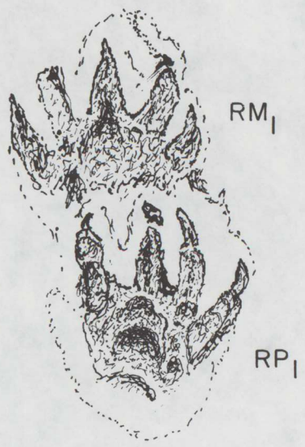


Plate 17. Tracks of an amphycyonid carnivore (*Axiciapes ferox* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-13). Pustulate features in the photograph are bubbles in the molding medium.

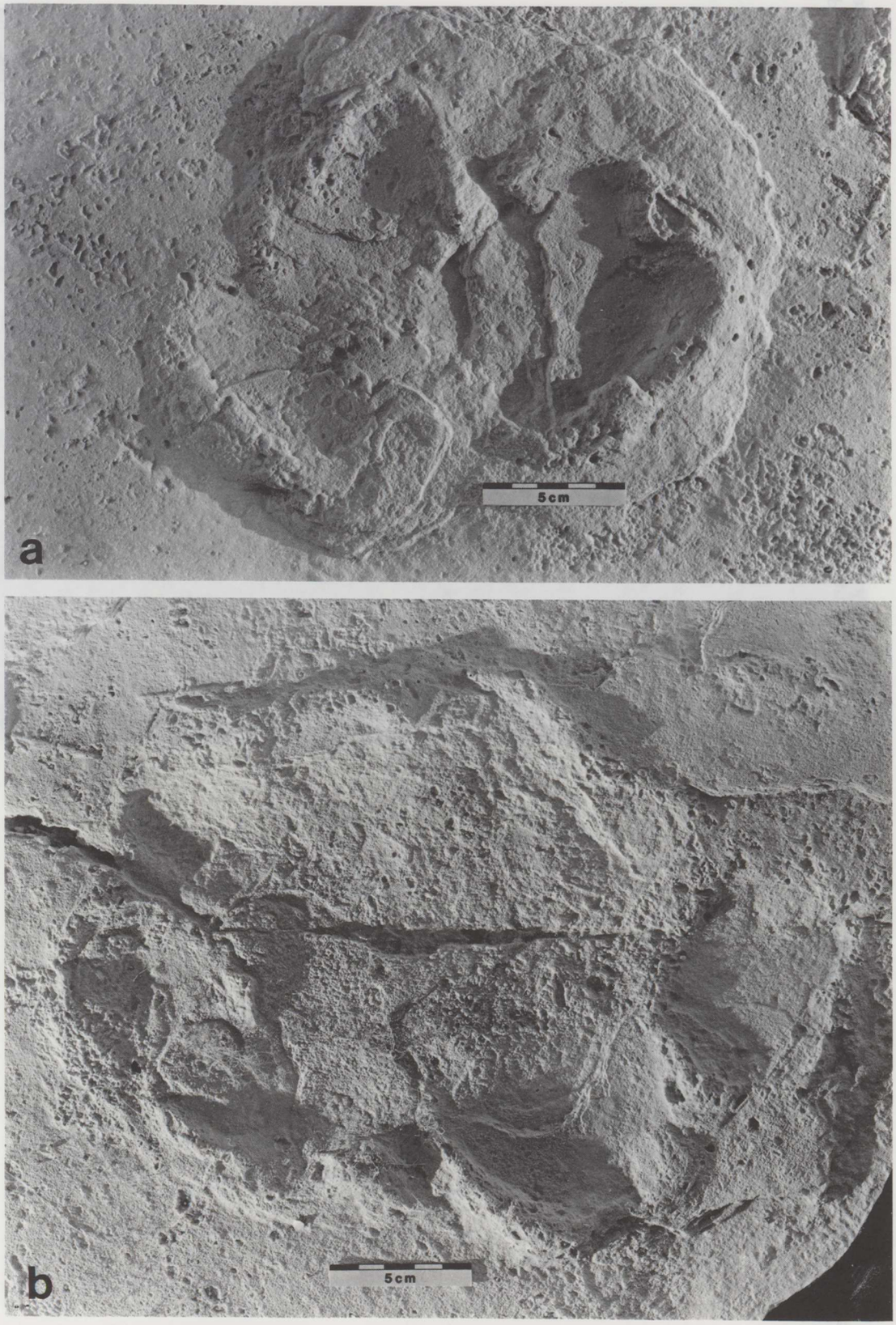


Plate 18. Footprints, possibly of a mesonychian (*Corymbipes superstes* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-34). (a) Left manus. (b) Left pes. (Note: Because of a different angle of illumination, the digits of the pes are seen more clearly in pl. 15b).

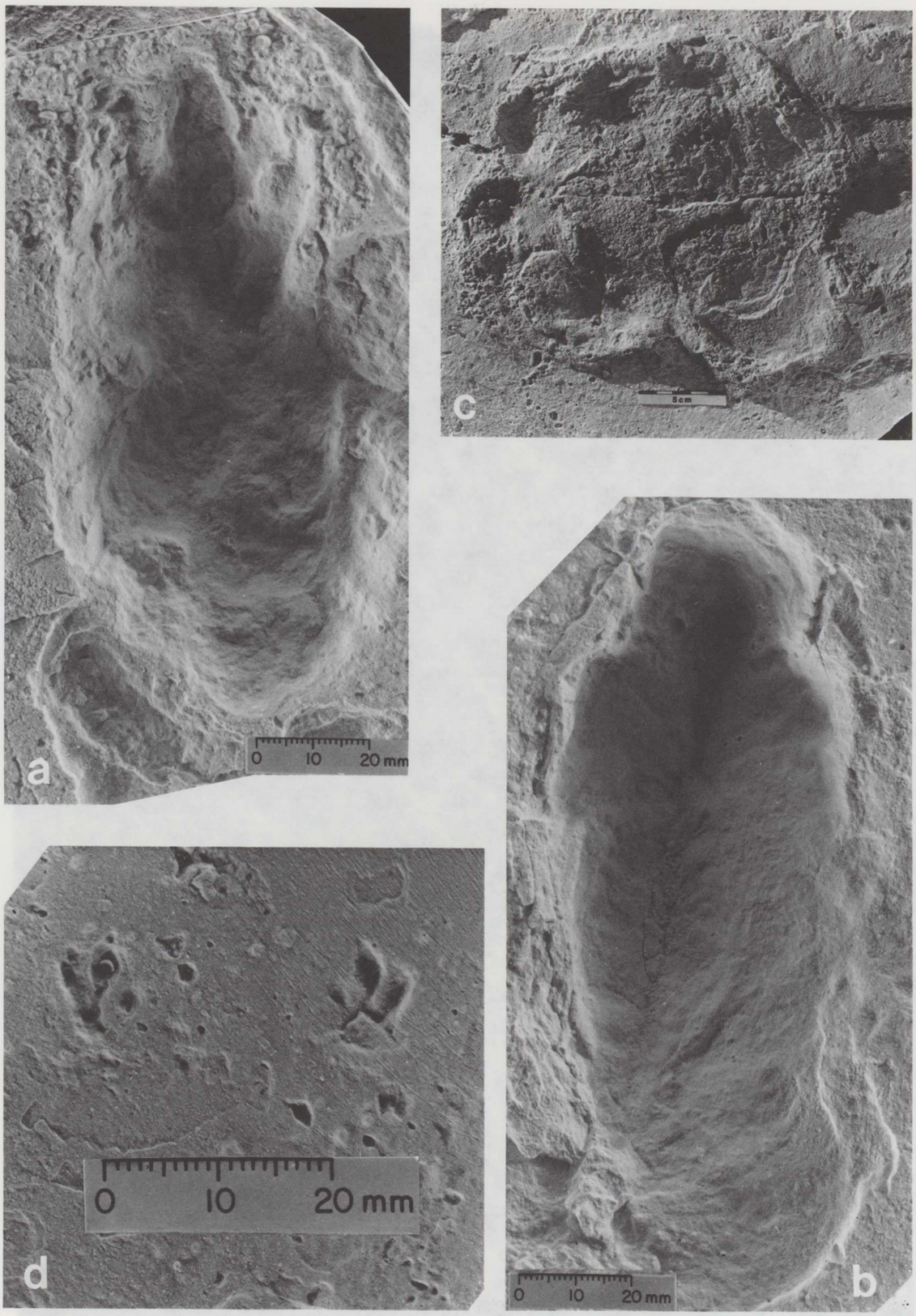


Plate 19. (a, b) Fore and hind foot impressions, respectively, probably of a cursorial rhinoceros (*Thrinaxopus hoplephoreus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-37). (c) Hind foot impression of a presumed mesonychian (*Corymbipes superstes* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-34). [Compare with pl. 18b]. (d) Footprints of a rodent (*Tricorynopus elaphrus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-41).

Plate 20. Perissodactyl or creodont footprints (*Palimmecopus praecursor* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-35). Right manus below, with right pes above almost superposed.

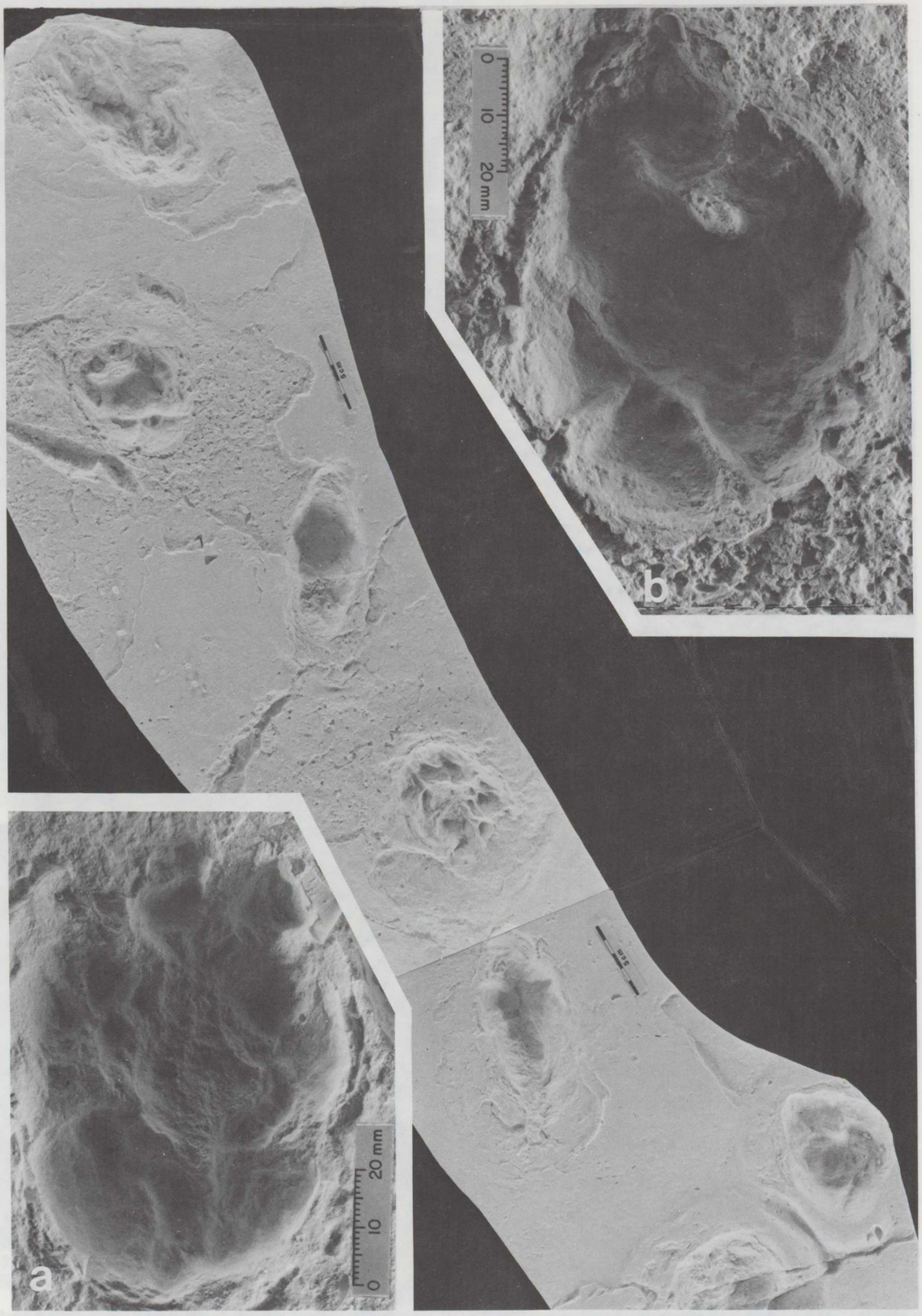


Plate 21. Footprints, probably of a tapiroid (*Apoxypus tessellatus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-36) and of a rhinocerotoid (*Thrinaxopus hoplephoreus* Sarjeant and Langston, ichnogen. et sp. nov. TMM 41500-37; see fig. 35 for key). a-b. *Apoxypus tessellatus* Sarjeant and Langston: (a) Left manus. (b) Right pes.

Plate 22. The irregular pattern of footprints of a presumed entelodont (*Anoplotheriipus zeuctus* Sarjeant and Langston, ichnosp. nov., TMM 41500-38) on section F, "Grand Junction" slab. [Compare pl. 4 for position.]

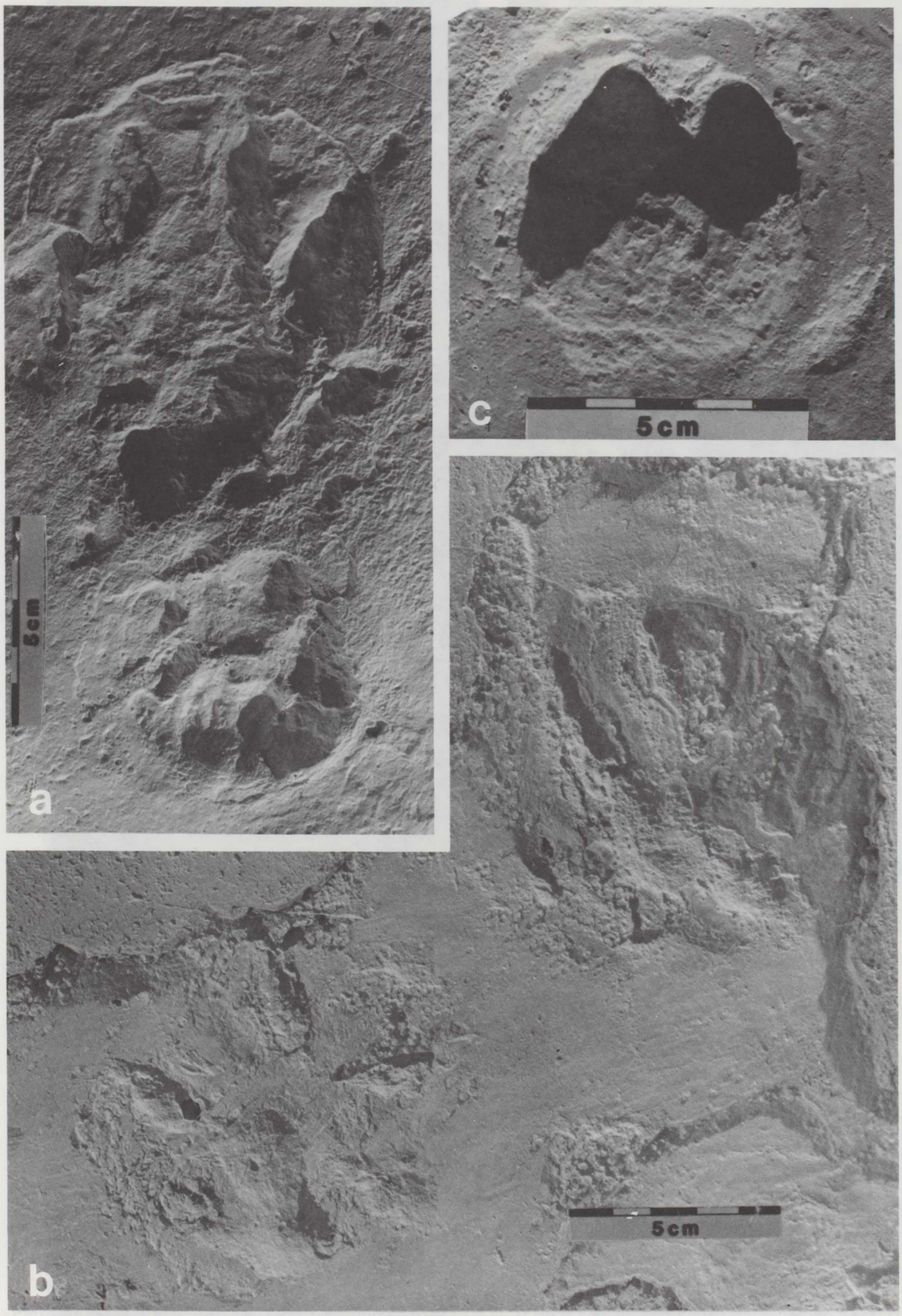


Plate 23. a-b. Footprints of a large ischyromyid rodent (*Ptyariopus aichmanticheirus* Sarjeant and Langston, ichnogen. et sp. nov., TMM 41500-43). (a) Impressions of right pes (above) and manus, infilled with sediment, the pes obscuring the manual digits. (b) Impressions of left manus (left) and right pes, not similarly obscured. (c) Single footprint of a presumed entelodont (*Anoplotheriipus zeuctus* Sarjeant and Langston, ichnosp. nov., TMM 41500-38).

Plate 24. Perissodactyl footprint, Type A, TMM 41500-45, cf. Brontotheriidae or Amynodontidae incertae sedis.

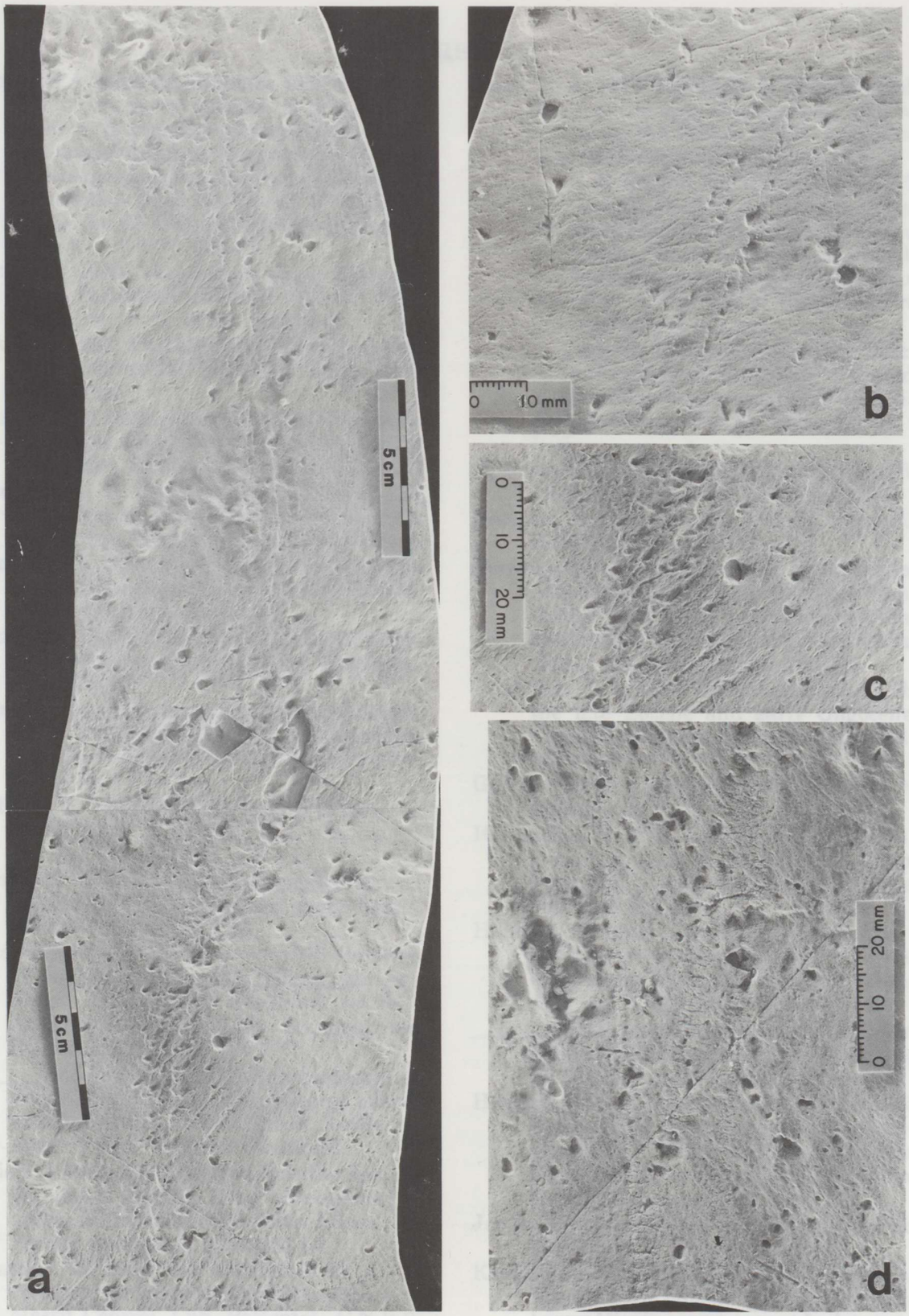
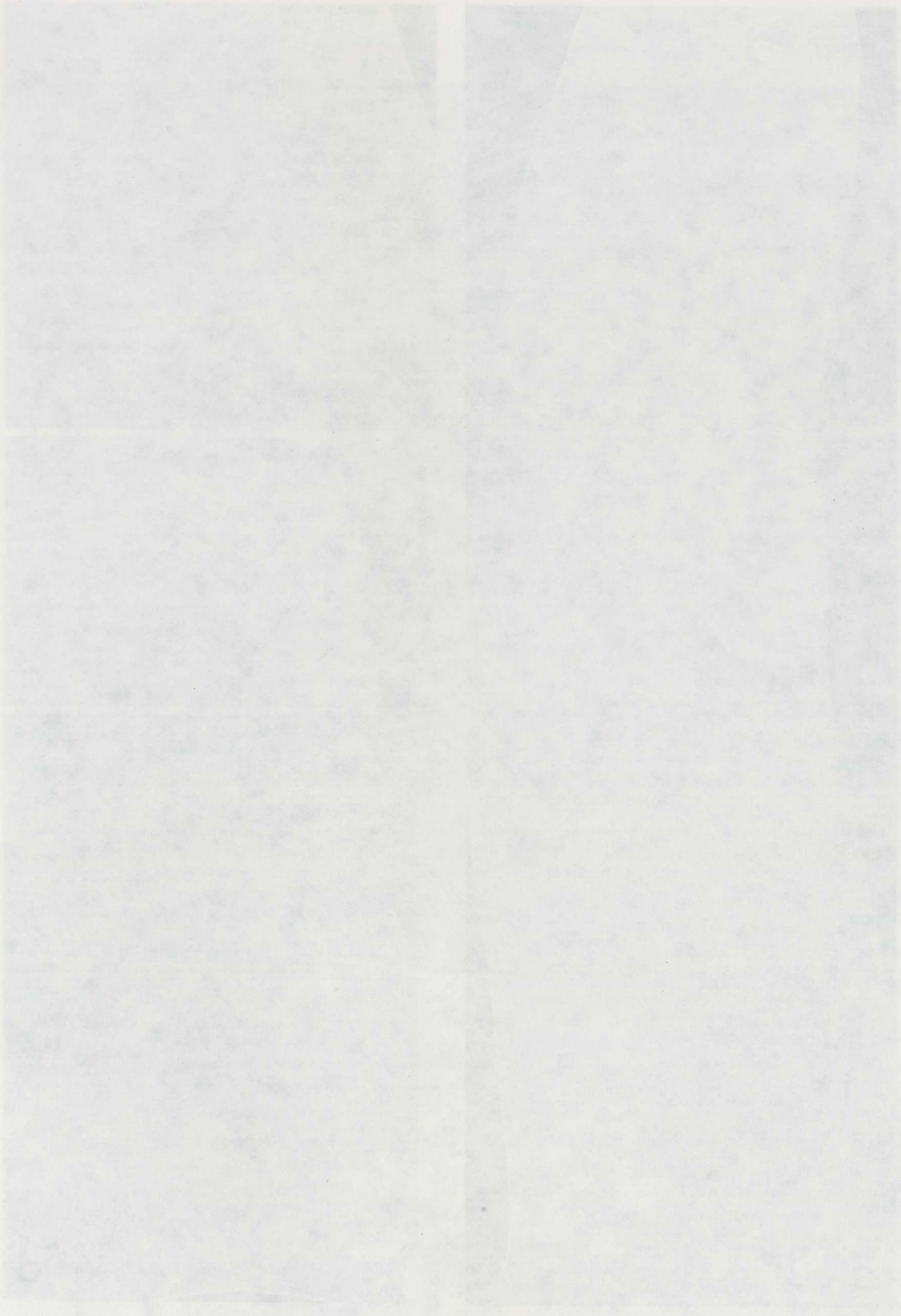


Plate 25. Invertebrate traces. (a) The whole trackway of Type A (TMM 41500-46) with below, Type B, a trace of uncertain character (TMM 41500-47). (b) Detail of the Type A trackway (corresponding to the uppermost part of (a)). (c) Detail of the Type A trackway (in the lower part of (a)), showing how faulty casting has produced apparent "spines" arising from it; these are not natural features and should not be taken into consideration in any morphological studies. (d) Detail of the Type B trace, turned through 90° to correspond with the orientation in fig. 51.



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